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CURRENTS OF THE AUDITORY CORTEX IN THE CAT

By

WOLFGANG KÖHLER, WILLIAM D. NEFF
AND JONATHAN WEGENER

AND

CURRENTS OF THE HUMAN AUDITORY CORTEX

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CURRENTS OF THE AUDITORY CORTEX IN THE CAT[1]

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University of Chicago, Chicago, Ill.

THIRTY-ONE FIGURES

In an earlier paper, Köhler, Held and O'Connell ('52; *cf.* also Köhler and Held, '49; Köhler, '51) have shown that, when objects appear in the human visual field, smooth potentials can be registered from the occipital pole of the intact head. The investigation was undertaken because certain facts in visual perception did not seem readily explainable on the assumption that cortical processes are restricted to the arousal and the propagation of nerve impulses (Köhler and Wallach, '44). Psychological evidence suggested that organization of cortical activities in perception is a field effect, and since the flow of currents in the brain as a volume conductor appeared to be the most likely effect of this kind, attempts were made to demonstrate such currents. This assumption is, of course, identical with the one formulated by Gerard and Libet (Gerard, '36; Gerard and Libet, '40; Gerard, '41; Libet and Gerard, '41).

We felt that, quite apart from the question whether the registered currents are actually responsible for visual organization, their occurrence as such had to be corroborated in further tests. For it could still be argued that, so long as records were taken from the surface of intact human heads, results remained too indirectly related to cortical processes,

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[1] This investigation has been supported by a grant from the Commonwealth Fund and by the Office of Naval Research. It has been carried out in the Laboratory of Physiological Psychology of the University of Chicago.

and could therefore be interpreted in several ways. We decided to take records from animal preparations in which the media intervening between the electrodes and the active tissue were largely or entirely removed. At the same time, the range of evidence was considerably widened by registering from the auditory rather than from the visual cortex.

The animals used in our tests were cats. While it was not particularly difficult to obtain clear results from most of our preparations, we fully realize that conditions upon which the outcome of tests in this field depends are very much in need of further exploration. The degree of cortical exposure, the depth of anesthesia, and the way in which the electrodes are attached obviously affect results. But we do not yet know the exact conditions under which good responses may be obtained, nor why, when an effort is made to keep experimental conditions as constant as possible, excellent responses may be obtained from one preparation while, with another, responses are less distinct and less regular.

PROCEDURE

The surgery necessary to expose the skull, to reduce its thickness or (in some animals) to expose the cerebral cortex was done under dial with urethane or, more often, under sodium pentothal anesthesia. In the former case, one-half of the injection was given intraperitoneally, the other half intramuscularly. Sodium pentothal was injected intravenously. In addition, pontocaine was locally applied when this seemed indicated. After a scalp incision had been made, the temporal muscle was cut along the superior attachment, and then laterally retracted to expose the skull.

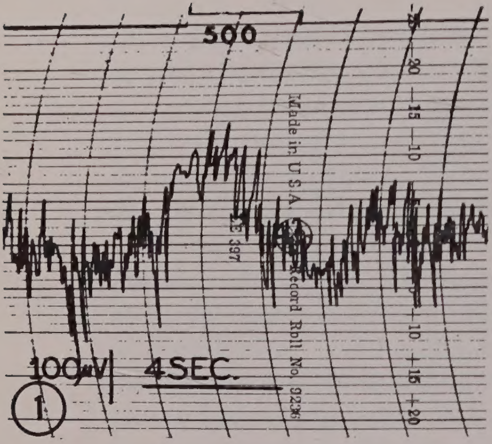
Some records were taken when the active electrode was attached to the intact skull; more generally, the skull over the auditory cortex was first made paper-thin by means of a large dental burr ($\frac{1}{4}$'' diam.) which was operated by a dental engine; in some preparations, the skull was entirely removed over the same area, and the electrode placed against the dura, or against the pia after removal of the dura.

We used electrodes of the silver-silver chloride type, inserted in a glass tube (Köhler, Held and O'Connell, '52, p. 296). When the active electrode was attached to bone by means of celloidin, it was filled with saline solution; when the brain was exposed, a gel consisting of a mixture of agar and saline connected the core of the electrode with the tissue. In the latter case, firm contact with the cortex was maintained by an electrode holder. The diameter of the actual contact surface was slightly less than .5'' when the electrode was attached to bone, but only about ⅛'' when the connection was made by means of the gel. The grounded electrode was placed either on the skin of the neck or on bone over the frontal sinus. This difference in its location did not affect the registered responses.

The cat was restrained by keeping the head fairly rigidly fixed in a head holder, and by fastening the limbs to an animal board. During experiments, the preparation was placed in a shielded, semi-quiet room. From here the leads extended to the amplifier and the recorder, which were located in an adjacent room. The D.C. amplifier, an instrument of the breaker type, has been described elsewhere (Liston, Quinn, Sargeant and Scott, '46; Köhler, Held and O'Connell, '52). It gives a perfectly stable account of slowly varying or steady potentials. In the output, the frequency of its breakers (75 cycles per second) is superimposed upon the steady flow. But these oscillations do not appear in curves taken with our recorder, a G. E. photoelectric instrument, which has a response time of .04 seconds. For the most part, stimulating sounds were produced by an oscillator (Wide Range Beat Frequency Oscillator, Type 700-A, General Radio Company) placed in the same room as the other instruments, and connected with a headphone (Permoflux PDR-8) which was suspended near one ear of the cat.

RESULTS

Under conditions of sound stimulation, smooth currents could be registered from 13 out of 15 cats tested. In this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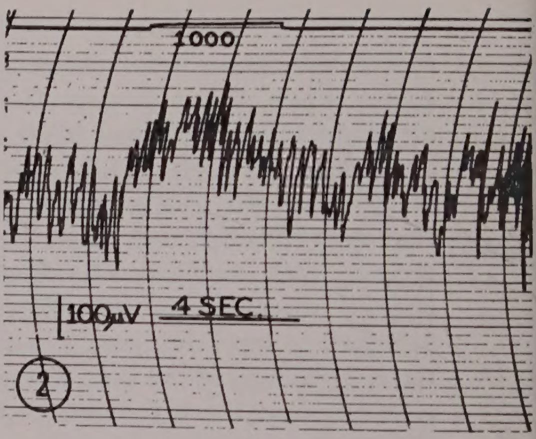
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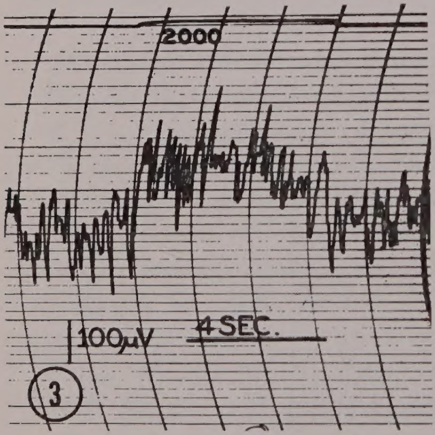
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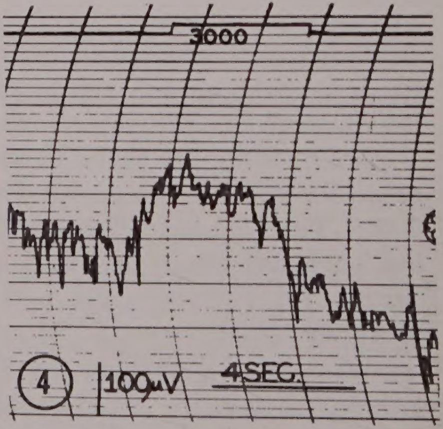
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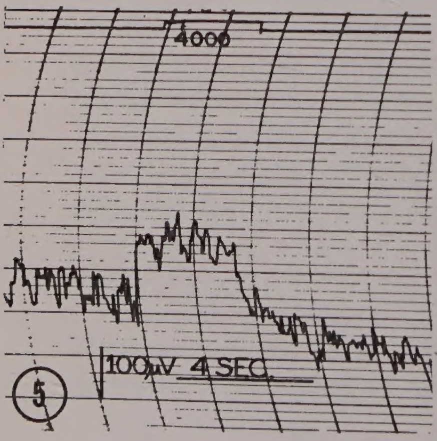
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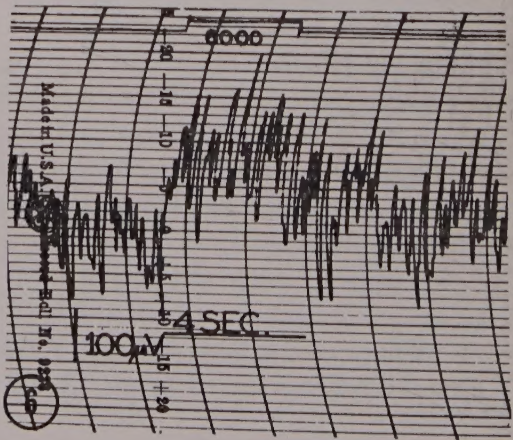
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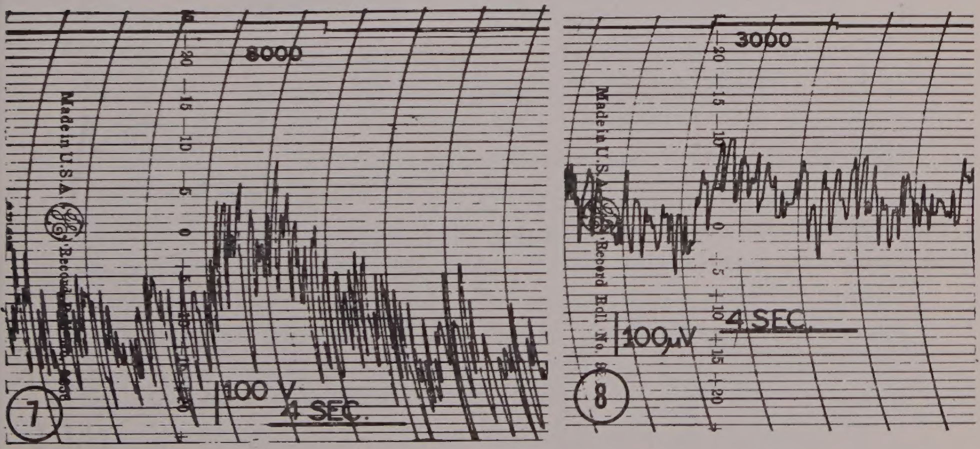
report, we will show curves from 10 preparations. All these curves were obtained when the effects of the anesthetic had largely subsided. This seems to be an important condition for good results. But it is probably not a sufficient condition. One of the two cats from whom we obtained no satisfactory responses was fairly alert at the time of the tests.

In preliminary experiments, the polarity of the cat's auditory responses had been found to be surface-negative in relation to the potential at the grounded electrode (Köhler, Held and O'Connell, '52, p. 325). This finding, which agrees with the polarity of auditory responses in man, but distinguishes the auditory responses of both species from human visual responses, has been confirmed in all our experiments. Records *1* to *7* show currents produced by tones of different frequencies. The sound pressure levels of the stimuli were in the range, 70 to 100 db. When records *1* to *7* were registered, the active electrode was attached to an extremely thin layer of bone left



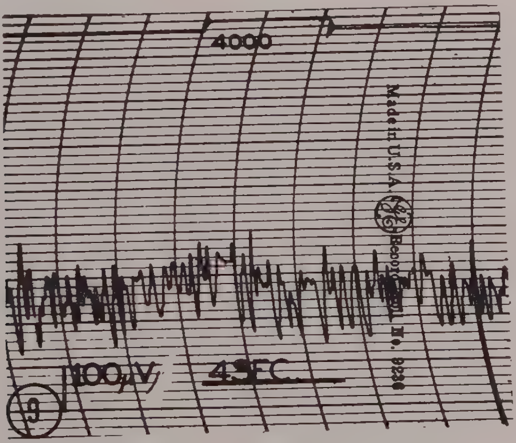
Records *1 to 8* Stimuli: 500 *(1,* cat 4), 1000 *(2,* cat 14), 2000 *(3,* cat 14), 3000 *(4,* cat 8), 4000 *(5,* cat 8), 6000 *(6,* cat 6) 8000 *(7,* cat 6) and 3000 ∼ *(8,* cat 11). Records *1* to *7* are taken with the active electrode attached to thinned bone over the auditory area, and the grounded electrode placed either on bone over the frontal sinus or on the skin of the neck. In records *1, 4, 6,* and *7* the active electrode is located over the middle ectosylvian gyrus, in records *2, 3* and *5* over the middle sylvian gyrus. Record *8* is taken from the exposed but intact skull over the middle ectosylvian gyrus. Anesthesia: Pentothal in all cases excepting record *1* (cat 4) where Dial with Urethane was used.

over the temporal region of the brain. In some instances, the electrode was located over the middle ectosylvian gyrus, in others, somewhat lower, i.e., over the middle sylvian gyrus. Irrespective of frequency, all these records show surface-negative responses. In terms of voltage, their size varies from about 100 to slightly more than 200 μV. As will be seen in other records, responses are sometimes considerably stronger. On the other hand, with some preparations, the size of the reactions seldom amounts to that of the present deflections. While records *1* to *7* cover only the four octaves from 500 to 8000 ~, clear responses have also been obtained when the frequency was considerably lower than 500 ~, and when it was as high as 20,000 cycles per second.

In a few tests made early in our investigation, we were unable to obtain convincing responses from a cat's head when the active electrode was placed on shaved parts of the intact scalp. In this respect, present results differ from those found with human subjects. We do not know whether the difference is caused by higher impedance of the intervening media in the cat, or by the fact that, with human subjects, no anesthetic is used. Occasionally, there have been responses when the electrode was attached to the exposed but intact skull of the cat. Record *8* may serve as an example.

The extremely thin layer of bone which was left intact between the brain and the active electrode in most animals seems to have little effect upon the registered responses. In fact, records *1* to *7* hardly differ from the curve shown in an earlier article (Köhler, Held and O'Connell, '52, p. 325), which was taken from the auditory cortex of cat 2 after removal of the dura.

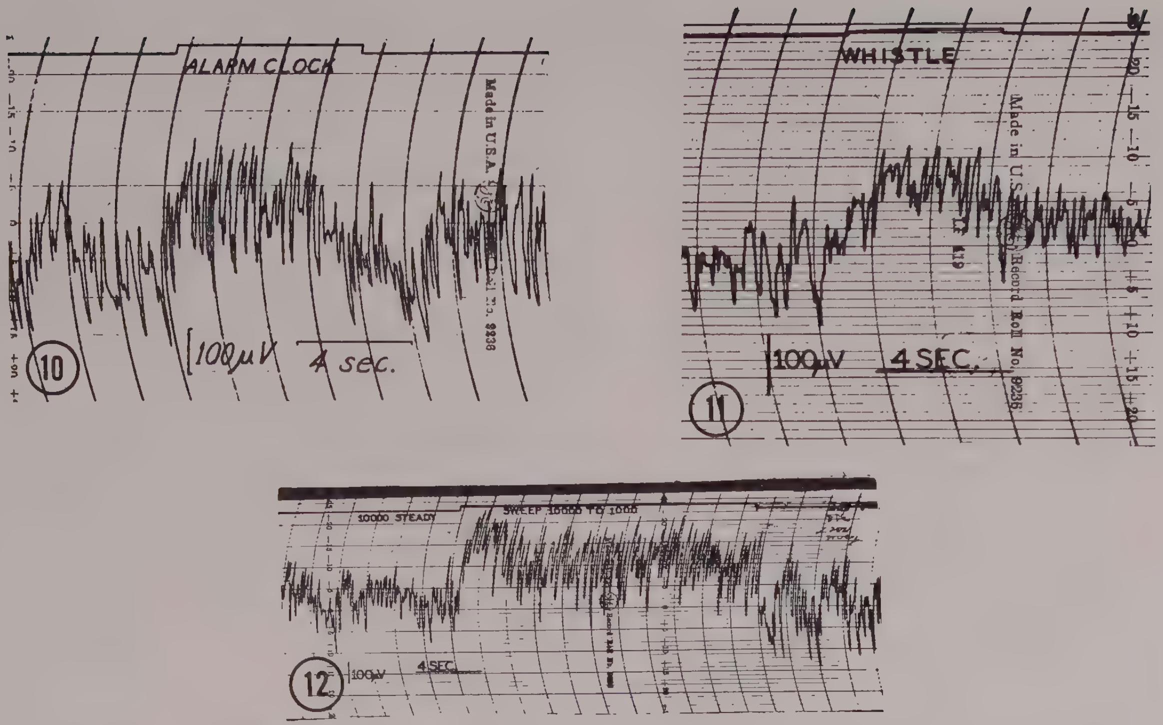
We have not tried to combine the demonstration of auditory currents as such with a study of frequency localization within the auditory cortex. An intense current spreads, of course, to some degree to the tissue around its source. Hence, if the location of this source is to be found, the intensity of the stimulating tone must be reduced, just as it is when evoked potentials are used for this purpose. Obviously, it would be more difficult under such circumstances to obtain convincing records of the currents *per se.* We have registered currents not only from several parts of the middle ectosylvian and the middle sylvian gyruses, but also from the posterior ectosylvian gyrus. Records *1* to *7* and those which will presently be shown will suffice as examples taken from the middle ectosylvian and sylvian gyruses. Record *41* of an earlier paper (Köhler, Held and O'Connell, '52), to which we have referred once before, was taken from the posterior ectosylvian gyrus.



Record *9* Absence of response to auditory stimulation when active electrode is placed on thinned bone over the foveal region of the visual cortex, and grounded electrode over the frontal sinus (*cf.* records *6* and *7* which are taken from the same cat (6), but with the active electrode placed over the middle ectosylvian gyrus). Anesthesia: Pentothal.

On the other hand, we have never obtained responses when the active electrode was placed on the posterior suprasylvian gyrus or on the visual area of the cat. For instance, when record *9* was taken, the active electrode was attached to a very thin layer of bone over the foveal region of the visual cortex of cat 6. There is no response in this record. And yet, the same cat gave at the same time one clear response after another when the active electrode was placed over the auditory area. Such negative results may mean that the currents of the auditory cortex do not spread very far into surrounding parts. But without further evidence no safe conclusion is possible in this respect. For, strictly speaking, these results only show that between the points tested in the posterior suprasylvian and lateral gyruses, on the one hand, and the grounded electrode, on the other hand, there is in such experiments no potential difference. This does not, of course, exclude the possibility that, at those points, potential differences drive an appreciable current through the tissue in another direction. We are not yet in a position to decide whether this is the case, or whether, with the active electrode attached to such points, no current is recorded because they are too far removed from the source.

Records *10* to *12* were taken under the same general conditions as records *1* to *7*, excepting that now stimulation had not the form of steady tones. There is no essential difference between the current caused by the noise of an alarm clock (record *10*) and the responses to steady tones. Sharp whistling produced by one of the experimenters always gave responses so long as the preparation reacted to any other sounds. Record *11* may serve as an example. In this curve, there is, for the first time, a slight indication of the initial positive deflection which other investigators have so often recorded (*cf.*, for instance, Brazier, '51, p. 127; Rosenzweig and Rosenblith, '53). The fact that, after this short deflection, it takes the negative flow considerable time to reach maximal intensity is obviously not important, because during this period the intensity of the stimulus may have grown. When record *12* was taken, the oscillator first produced a steady tone of 10,000 ~, and then a ''sweep'' followed which brought the frequency down to 1000 ~ within about 18 seconds. On the signal line the duration of this sweep is marked. The record shows that a strong current developed almost as soon as the steady tone was replaced by lower changing frequencies, and that this current hardly decreased until, a quarter of a minute later, the sweep had ended at the constant frequency of 1000 ~. At maximal intensity, the response amounts to about 300 μV. It is clearly accompanied by an intensification of the spon-



Records *10* to *12* Responses to the noise of an alarm clock *(10,* cat 6), to whistling *(11,* cat 14) and to a "sweep" from 10,000 to 1000 ~ *(12,* cat 6), registered from thinned bone over the middle ectosylvian gyrus *(10)*, and the middle sylvian gyrus *(11* and *12)*. Anesthesia: Pentothal. Note that in record *12* stimulation enhances the cortical rhythm.

taneous cortical rhythm. The sudden decrease of the response at the end of the sweep (and the beginning of the steady tone) may be caused by a rapid growth of electrotonic obstruction; but local fatigue may, of course, also be involved.

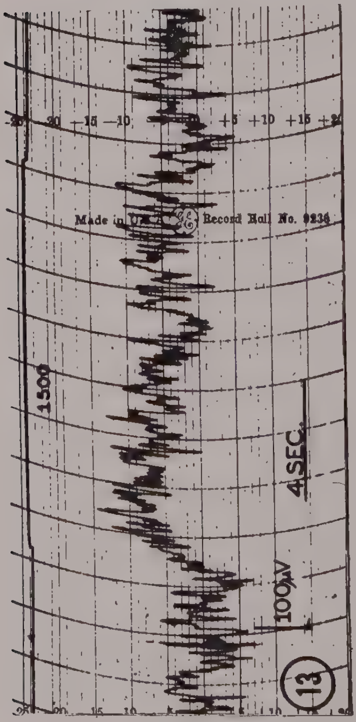
The temporal characteristics of responses to steady tones vary a great deal from one record to another. In some instances, the current reaches its greatest intensity so fast that, with the paper speed used in our experiments (.75 cm per second), the first ascent appears as quite abrupt. In other curves, such as that of record *2,* the greatest intensity develops more slowly. At least in one curve (record *3*), a steep first ascent occurs after an appreciable latency time. Equally varied is the form of the responses after their greatest size has been reached. Thus, in record *2,* the current begins to decrease before the end of stimulation. On the other hand, it clearly persists beyond this moment in record *6*.

Such variations are even more striking in the following curves (records *13* to *20*). Records *13* and *15,* for instance, show once more that the auditory currents may develop fairly slowly. Records *13* and *14* demonstrate that the flow sometimes persists during long periods of stimulation without losing much of its intensity. When record *13* was taken, the stimulation period amounted to 13.5 seconds, and in the experiment of record *14* to no less than 22 seconds. In both curves, the response declines very slowly. Records *15* and *16* agree with record *6* in showing that responses may even persist beyond the end of stimulation. In record *15,* there is a sharp reduction of the flow just when the tone of 1000 ~ is discontinued after 7 seconds; nevertheless, the level remains fairly high for some time afterwards. Again, in record *16* the response declines to some degree during the second part of the stimulation period; but the current does not disappear entirely until several seconds after the end of the tone. However, the decrease of the response may begin very early. This is clearly shown in records *17* and *18,* but still more strikingly in records *19* and *20* where, a few seconds after the beginning of stimulation, no steady flow seems to be left. In some of these curves, the decline is made particularly impressive by the fact that the initial response is strong. It amounts to approximately 400 μV in records *18* and *20*.

We do not know why an appreciable current sometimes continues to flow when stimulation has ended. But the fact that, in the beginning of stimulation, responses may develop slowly and the observation that they tend to decline before stimulation is discontinued can perhaps be derived from well-known concepts of classical neurophysiology. According to these concepts, any current which spreads in nervous tissue soon establishes electrotonic effects in this tissue. In the long run, it is the anelectrotonic effect which prevails (Ebbecke, '22). This effect has the character of an obstruction. When it arises, the distribution of the current undergoes a corresponding change. The current is gradually reduced in parts in which it was first particularly intense, and it grows in parts in which it was first weaker. Now suppose that in a given test the active electrode is not optimally located in relation to the source, and that, as a result, the flow is at first stronger in other parts than it is at the place of the electrode. Under these circumstances, electrotonic action must gradually weaken the flow in the former parts, and strengthen it at the electrode. From this point of view, the gradual growth of the response in some of our records would be merely an example of "electrotonic spread."

We doubt whether this is the only factor which is here involved. The first ascent of the response may also be retarded as a result of anesthetic action; moreover, the animal may happen to be half asleep when stimulation begins, and may then be alerted by its impact.

It follows from the very nature of electrotonic spread that, once the registered current has grown to considerable size, its intensity will again be reduced. For now anelectrotonic obstruction will weaken the flow which arrives at the active electrode, and eventually the registered response may even disappear in this fashion (*cf.* records *19* and *20*). When thus interpreted, disappearance of the registered current



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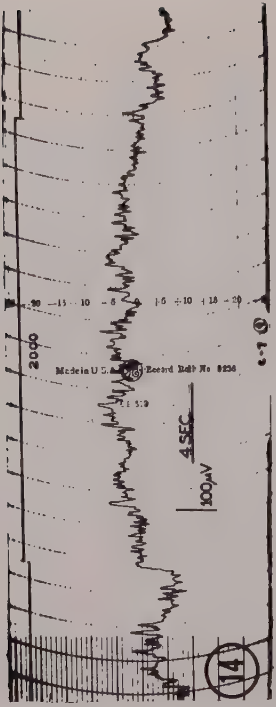

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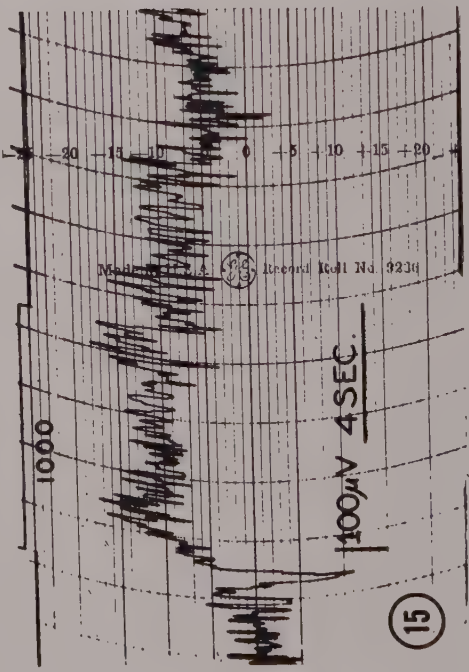

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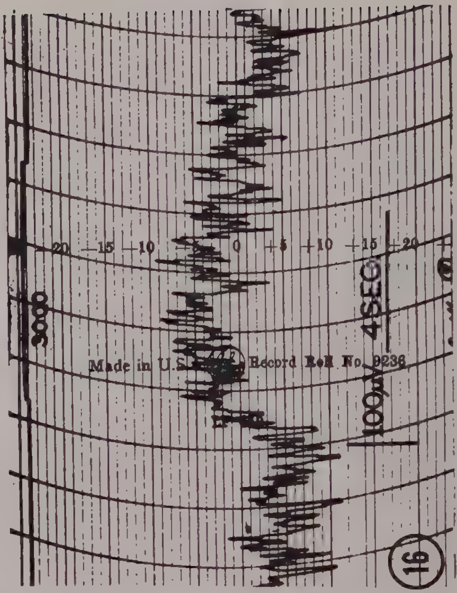

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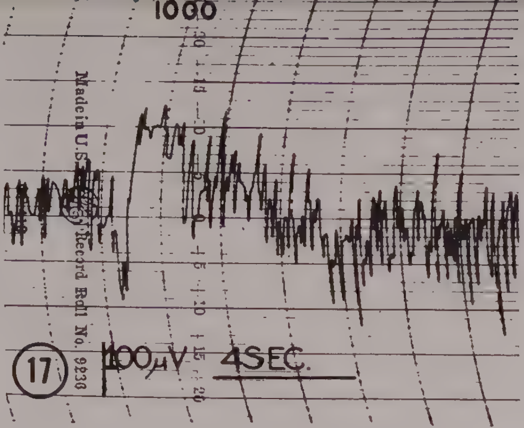
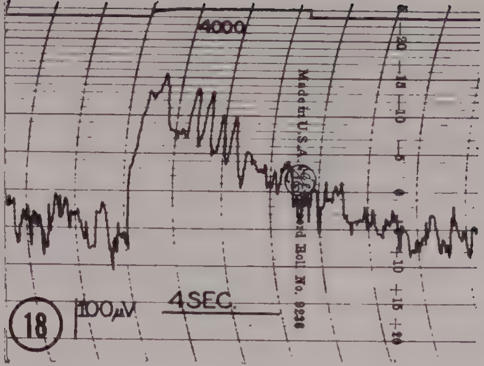
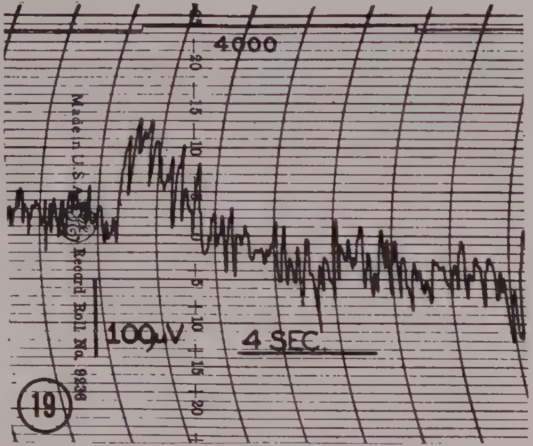
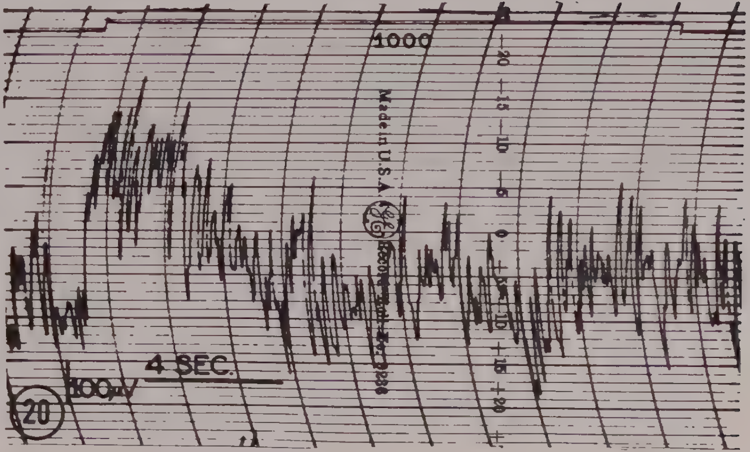






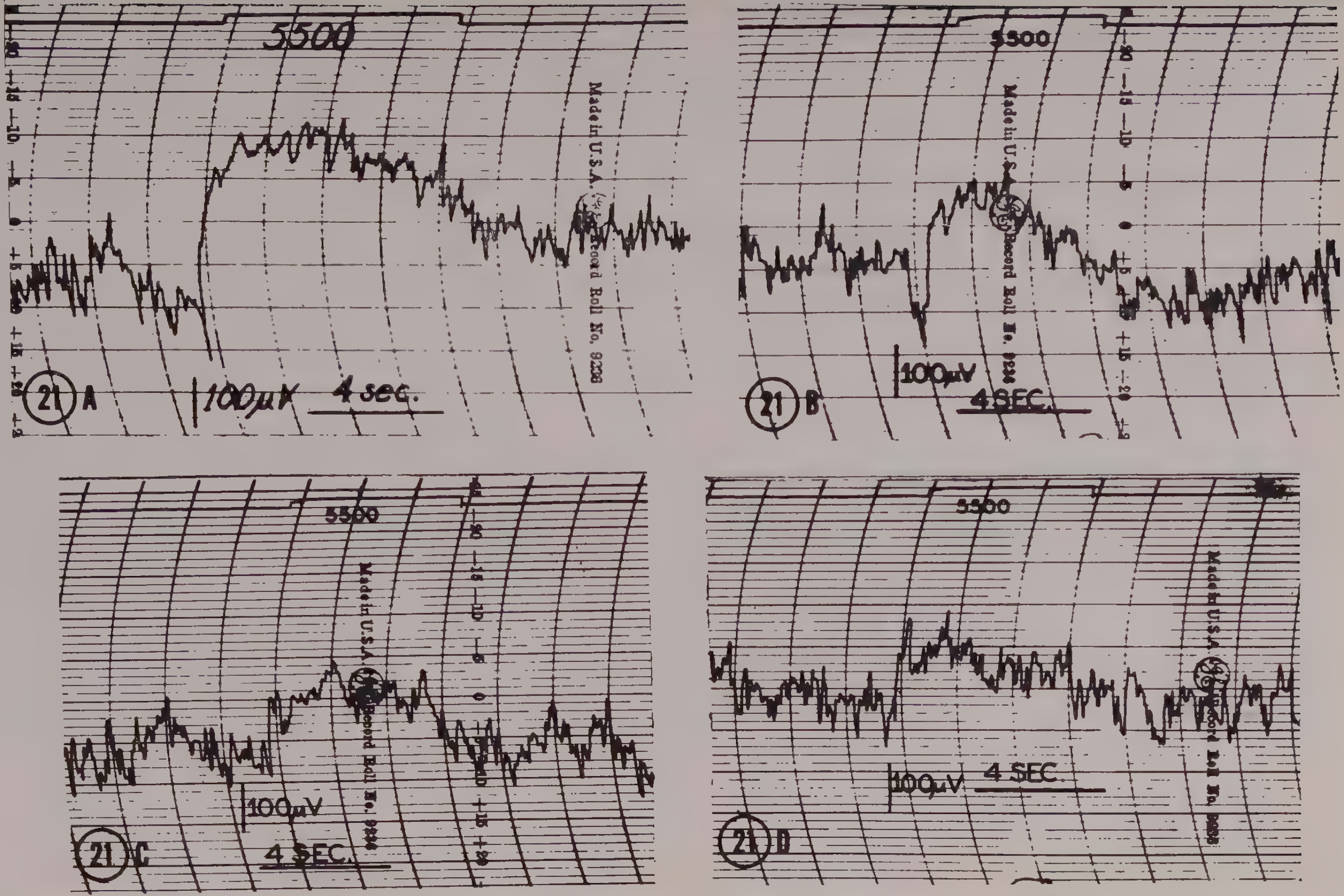


Records *13 to 20* Stimuli: 1500 *(13,* cat 14), 2000 *(14,* cat 7), 1000 *(15,* cat 4), 3000 *(16,* cat 14), 1000 *(17,* cat 4), 4000 *(18,* cat 8), 4000 *(19,* cat 12) and 1000 ~*(20,* cat 6). Active electrode placed on thinned bone over middle ectosylvian gyrus in *19* and *20,* over middle sylvian gyrus in records *13* and *16* to *18,* and over anterior ectosylvian gyrus in *14.* Anesthesia: Pentothal in all cases excepting *15* and *17* where Dial with Urethane was used. Note the persistence of the responses in *13* to *16,* the rapid decline of the responses in *17* and *18,* and their early disappearance in *19* and *20;* also the initial positive wave in *15* and *17.*

during stimulation would mean only that the intensity of the particular flow which reaches the active electrode is no longer great enough to be recorded, while the cortical current as such may still be fairly strong in other parts.

Any theory of the gradual decline will have to take account of the following observations. Once the response to a given tone is weakened, this effect tends to persist for some time. In one test we gave the tone 5500 ~ for 7 seconds, and then repeated stimulation by this tone 14 times with intermissions of 10 seconds. The second and all later stimulation periods amounted to about 5 seconds. All 15 tones established currents. It will suffice if we show only four of these responses, the first, the second, the tenth and the last; because, beginning with the third, their characteristics varied little. In record *21A,* the current rapidly develops to maximal intensity; but during the second half of the stimulation period its size is gradually reduced. The greatest deflection corresponds to about 350 μV. Record *21B* closely resembles *21A,* excepting that now the greatest deflection is reduced to one-half of what it was before, and that from this level the curve descends more rapidly. Records *21C* and *D* illustrate the fact that, while the form of later responses differs somewhat from the one shown in records *21A* and *B,* their size is hardly smaller than that of the second response. It therefore appears that, once the intensity of an auditory current has been greatly reduced by its own effect upon the tissue, this very fact operates against a further weakening when the stimulus and the current are now repeated. On the other hand, there seems to be little, if any, recovery during rest periods of ten seconds. Obviously, it is not advisable to make many tests with a given tone in a rapid sequence, unless one intends to study precisely such after-effects.

Two further phenomena which sometimes appear in our curves have so far been mentioned only in passing. In the first place, the initial positive wave which has so often been recorded by others appears not only in record *11,* but also, and far more clearly, in records *15, 17,* and *21B.* Record



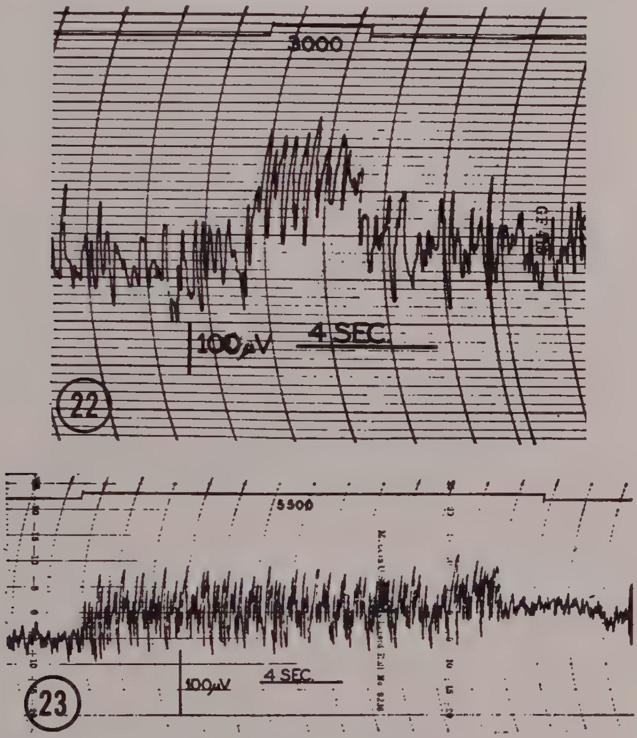
Records *21* a–d The first, the second, the tenth and the fifteenth response to repeated stimulation by the tone 5500 ∼. Note the smaller size of all responses after the first; also the initial positive wave in *21 b*. Cat 8. Anesthesia: Pentothal. Active electrode on thinned bone over middle sylvian gyrus.

24, which will presently be shown, contains a further example, and we could add several others. The fact that the initial positive wave has not been registered more regularly is probably caused by our instruments. A recorder with the response time .04 seconds is too slow for an adequate recording of this short wave. Moreover, the oscillations intrinsic to the operation of our amplifier, which have a length of approximately 13 msec, may interfere with the initial neural wave.

A second phenomenon to which we have so far hardly referred is a change of the spontaneous rhythm under the influence of sound stimulation. As many of our curves show, the spontaneous rhythm as such can readily be registered with our instruments. In fact, sometimes its amplitude in our records is so great that the oscillations threaten to obscure the smooth responses (*cf.* records *6* and *7*). The rhythm can, of course, be depressed by deep anesthesia. But once this has happened, it is also difficult, if not impossible, to obtain satisfactory records of auditory currents. It does not, of course, follow that, conversely, the currents must always be obtainable when a more or less normal rhythm is registered. Actually, the currents are more easily disturbed by adverse conditions such as anesthesia than the rhythm is. In our experiments, the oscillations were sometimes fairly strong when no auditory currents could be recorded.

Rheinberger and Jasper ('37) found that sounds tend to enhance and to regularize rather than to block the rhythm of the auditory area. A few years later, Bremer ('43) confirmed this fact in a most thorough investigation. According to him, the rhythm is not only intensified and regularized, but also accelerated by sounds. More recently, Tunturi ('49) once more made the same observations.

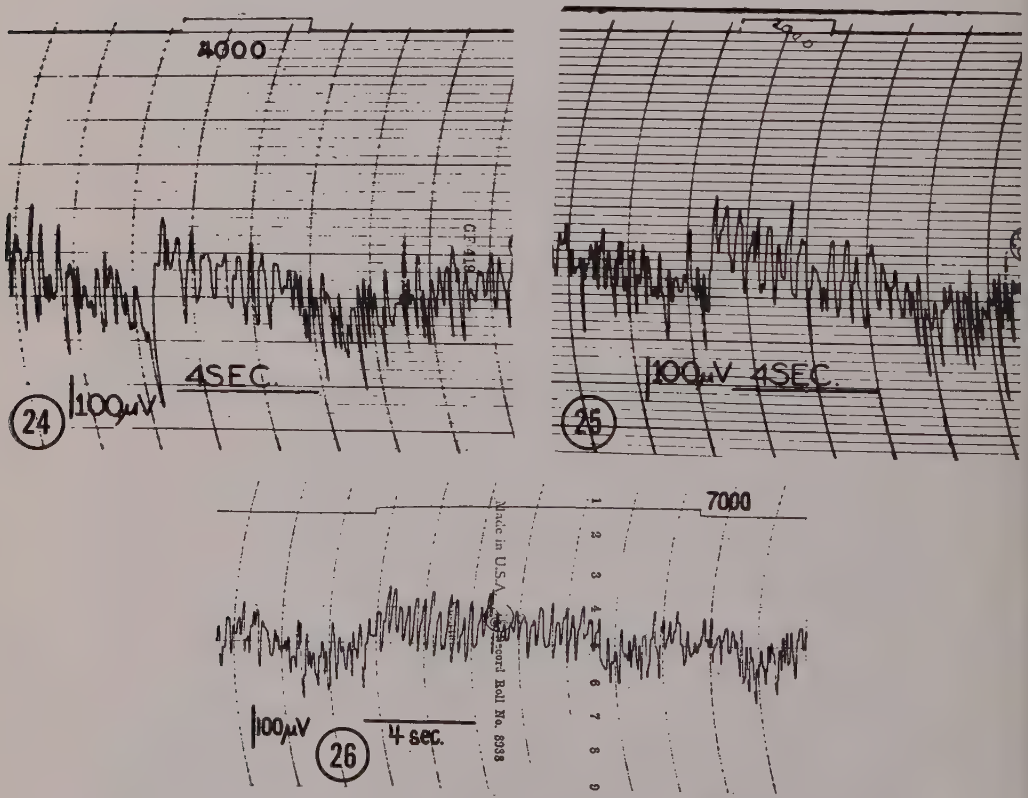
Intensification of the rhythm by sound stimulation occurred repeatedly in our experiments. The change is obvious in record *12.* It also appears in record *22,* and is most obvious in record *23.* Regularization of the oscillations was fairly frequently observed. It is shown in records *22, 24, 25* and *26.* The fact that not all our curves exhibit intensification of the rhythm may again be caused by the characteristics of our instruments. If, as Bremer and Tunturi have shown, sounds considerably accelerate the spontaneous waves, the higher frequencies which thus originate will not often be registered by our slow recorder, and as a result the intensification of such accelerated oscillations can for the most part not appear in our records. This is particularly true in view of the fact that the stimuli used in our experiments were generally quite intense. Bremer reports that, with high intensities, the frequency of the waves may grow to 70 cycles per second, which is far beyond the range of our recorder. In addition, the oscillations intrinsic to our amplifying procedure are likely to interfere with such



Records *22* and *23* Responses with accentuation of the cortical rhythm (*cf.* also record *12*). Record *22* taken from the middle sylvian gyrus of cat 6, and record *23* from the middle ectosylvian gyrus of cat 7. Anesthesia: Pentothal.

high neural frequencies. These factors do not prevent regularization of the rhythm from appearing in our records. The regular waves shown in records *24* to *26* can hardly be said to be accelerated. Their frequency appears to be about the same as that of the main rhythm before stimulation, and the greater regularity of the waves during stimulation makes the impression of being caused by the disappearance of inharmonic higher components from the curves. Incidentally, record *24* shows one more example of the initial positive wave.

The interpretation of our records as demonstrating that sounds produce currents in the auditory cortex may seem to

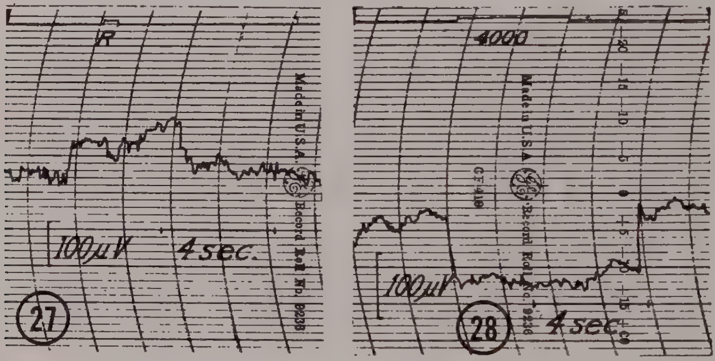


Records *24* to *26* Responses to 4000, 2000 and 7000∼ with regularization of the cortical rhythm. Records *24* and *25* taken from the middle sylvian gyrus of cat 4, record *26* from the posterior ectosylvian gyrus of cat 2. Note the initial positive wave in record *24*. Anesthesia: Dial with Urethane.

be open to the following criticism. Not only the presentation of visual objects but also that of tones and noises may cause eye movements. But any change in the direction of the eyes tends to give rise to currents which originate in the eyes themselves, and then spread across large parts of the head. It might therefore be argued that the currents shown in our records issue from these sources rather than from the auditory cortex. Since this issue is of great importance to all work on cortical currents in which animals serve as subjects, it must now be discussed in some detail.

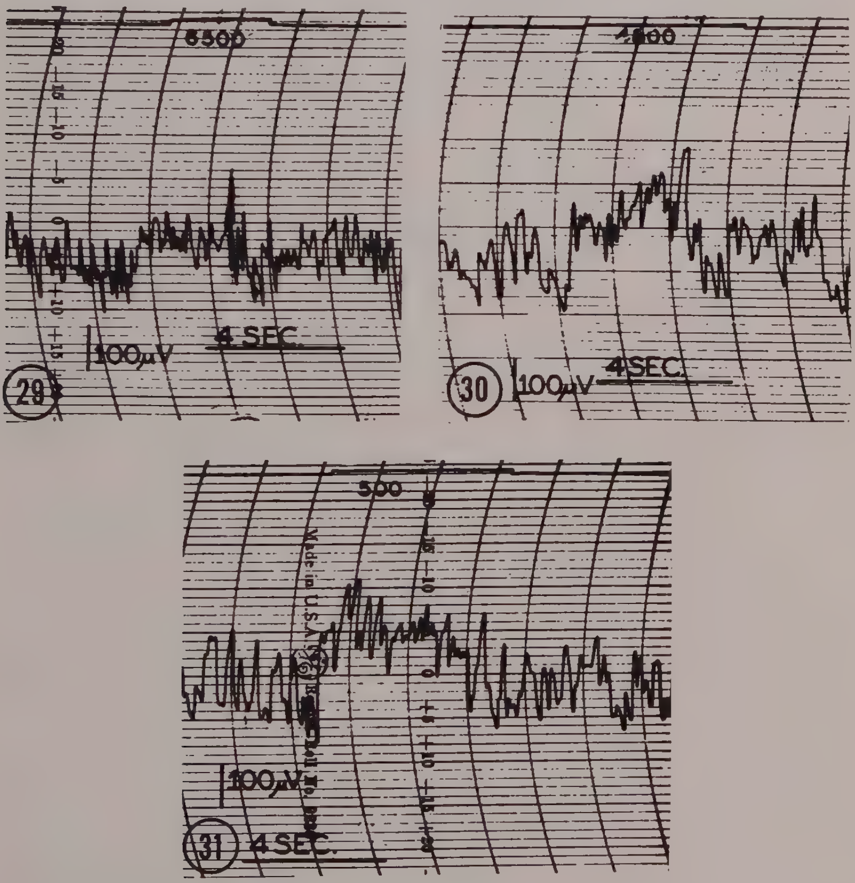
The eyes of the cats with whom we worked were often carefully watched for long periods. Occassionally, slow eye movements occurred spontaneously; we also elicited such movements by moving food before the animals' heads. Generally speaking, the amplitude of the movements was small, and during experiments their occurrence did not regularly coincide with the responses registered during sound stimulation. We could, however, take records of the currents which accompanied such movements, and found that results agreed entirely with those of other investigators. Mowrer, Ruch and Miller first demonstrated in 1936 that these currents originate within the eye rather than in the extrinsic ocular muscles (13). More specifically, they found, the currents are maintained by the resting potential of the eye which keeps the retina negative in relation to the cornea. The resulting flow emerges in front, and then spreads backward on the surface of the head. Naturally, when the eyes turn one way or another, the distribution of the flow changes, but now remains the same until the eyes turn back again. When two electrodes are attached to the head in a transverse orientation, the potential at the one on the right side becomes more positive as soon as the eyes turn to the right. The opposite effect occurs when the movement is toward the left side.

In our tests, the electrodes were attached to shaved parts of the intact head, the active electrode over the left auditory area and the grounded electrode farther backward on the right side of the median plane. In the records, a deflection downward was therefore to be expected when the eyes turned to the left, and a deflection upward when they turned to the right. Numerous tests confirmed these predictions. It will suffice if we show two examples. When record *27* was taken, food was moved from the left to the right before the cat's head, and the cat promptly turned his eyes in the same direction. The record shows the expected deflection upward. This deflection begins before the signal on top because the signal was given immediately after the movement had actually begun. In record *28,* the movement of the eyes was caused by intense sound stimulation on the left side. A fraction of a second after the beginning of stimulation the animal turned his eyes abruptly to the left, and kept them turned until after stimulation had ended. The corresponding deflection downward is clearly shown in the record. It cannot be interpreted as a response of the auditory cortex, because the active electrode was attached to the intact scalp, and because the polarity of this response is positive at the active electrode.



Records *27* and *28* Currents produced by deviation of the eyes to the right *(27)* and to the left *(28)*. The electrodes are placed on the intact head in a transverse arrangement, the active electrode on the left side. Cat 11. In record *27* the cat's eyes follow food which is moved toward his right side; in record *28,* they turn toward a tone given on the left side.

Can the consistently surface-negative responses to sound which are shown in this report be explained as the results of eye movements? Since, with a given position of the electrodes, stimuli were sometimes given on the right and sometimes on the left side, this seems extremely improbable. Nevertheless, we decided to subject the issue to experimental tests. Because of the fact that the currents which accompany eye movements originate within the eye, these currents must disappear when the eyes are removed. Responses to sounds which are registered when this operation has been performed



Records *29* to *31* Auditory currents recorded from cat 14 *(29)* and cat 15 *(30* and *31)* after removal of the eyes. The active electrode is placed on thinned bone over the middle sylvian gyrus. Anesthesia: Pentothal.

can therefore not be interpreted as such currents. We removed the eyes of two cats from whom many good records had previously been taken, and resumed recording when the deep anesthesia necessary for the operation seemed to have sufficiently subsided. Both animals now gave the same responses to sounds as had been obtained before the operation. As an after-effect of the operation as such, or because the anesthesia was still deeper than it had been before, the intensity of the currents was, on the whole, somewhat reduced; but since we had no difficulty in registering one clear response after another, experimentation was discontinued when their number left no doubt as to the main result. Currents of eye movements may occasionally be added to, or substracted from, the responses which are recorded from the auditory cortex; but there can be no essential relation between the two facts. Records *29* to *31* may serve as examples of the curves obtained after removal of the eyes. In both preparations, the active electrode was placed on a thin layer of bone over the middle sylvian gyrus, and the grounded electrode on a shaved part of the neck. In record *29,* which was taken from cat 14, the size of the deflection corresponds to about 100 μV. In records *30* and *31,* which were taken from cat 15, the potentials are approximately 150 and 200 μV.

SUMMARY

1. During stimulation by sounds a smooth electric flow can be registered from the auditory cortex of the cat. No such responses to sounds have so far been obtained from other areas of the cat's brain. The extent to which currents of the auditory cortex spread in the brain has not yet been clearly established.

2. The temporal characteristics of auditory currents vary greatly. Their onset is fairly abrupt in some cases, but more gradual in others. The flow may persist for long periods, occasionally even beyond the end of stimulation; but it may also soon become weak, and it sometimes disappears before stimulation is discontinued.

3. It seems that good records can be registered only under rather light anesthesia. It is our experience that no convincing responses are obtainable so long as the anesthesia markedly depresses the spontaneous cortical rhythm.

4. Within the limits imposed by the characteristics of our instruments, it has been confirmed that sound stimulation tends to enhance rather than to block the spontaneous rhythm of the auditory area.

5. The currents which are registered from the auditory cortex cannot be interpreted as currents which accompany eye movements. The potentials of the auditory cortex are not essentially affected by removal of the eyes.

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CURRENTS OF THE HUMAN AUDITORY CORTEX[1]

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TWENTY-SEVEN FIGURES

When records of auditory currents are taken from the intact heads of human subjects, results will, in a technical sense, always be inferior to those registered from an animal's brain, because in the latter case the distance of the active electrode from the auditory cortex can be reduced to a minimum. But the study of such currents in man also offers certain advantages. For in man the currents can be recorded when the brain is not affected by an anesthetic. Moreover, since human subjects can be asked to fixate a given mark, the danger that currents which accompany eye movements appear in the records is greatly reduced. We should like to add that, while the active electrode is surely not in an optimal position when it is placed on the intact head, this very fact may lead to important information as to the spreading of cortical currents in the brain. Only a few records of human auditory currents are so far available (Köhler, Held and O'Connell, '52, pp. 324 f.). It therefore seemed to us that a further study of such currents was indicated.

The general conditions under which currents of the human cortex have previously been registered need not again be described in detail. In the present investigation, we used the same instruments as before, and also non-polarizable electrodes of the same type (Köhler, Held and O'Connell, '52, p. 296). The glass tubes of the electrodes were firmly attached to the scalp, and filled with saline. Early in our work, the active electrode was attached to a region above the ear, under which the auditory cortex was presumably located, and the grounded electrode to the vertex, where it had also been placed in experiments on human visual currents.

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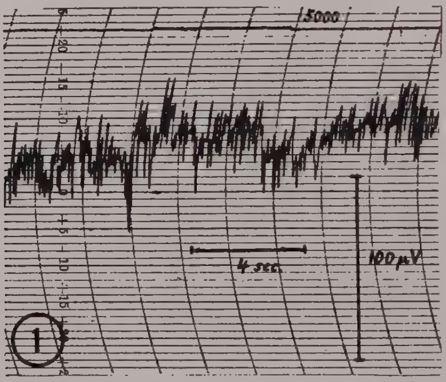
[1] This investigation has been supported by a grant from the Commonwealth Fund.

With the electrodes arranged in this fashion, one sometimes obtains records of auditory currents which greatly resemble those taken from the cat's auditory area, excepting that the human responses are, naturally, much weaker. Record *1*, which we reproduce from an earlier report, is a good example.

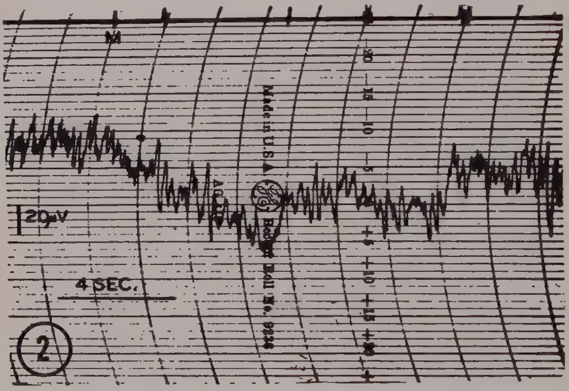


Record *1* Subject Ec. Response to the tone 5000 ~, recorded with the active electrode placed a few centimeters above the meatus, and the grounded electrode on the vertex.

It also shows the initial positive deflection which often appears in the auditory responses of the cat's brain (Köhler, Neff and Wegener, '55). On the whole, however, results are not satisfactory under these conditions, particularly since they vary considerably from one subject to another. With some individuals, it seems almost impossible to obtain plausible responses when the electrodes are placed as indicated. With others, records clearly show reactions to auditory stimulation; but the form of such responses suggests the presence of complicating factors. The complication consists in the fact that a first weak current in one direction is soon followed by a stronger and more persistent current of the opposite polarity (Köhler, Held and O'Connell, '52, p. 324). Now, the geometrical relation between the human auditory cortex and the surface of the head is by no means simple. Thus the suspicion arose that the difficulty might be caused by inadequate positions of the electrodes.

A chance observation made when visual rather than auditory currents were being recorded confirmed this suspicion. In such experiments, an object was slowly moved across the field by a motor. Under these circumstances, the first response sometimes occurred too early, that is, not when the object just appeared in the periphery, but rather as soon as it began to move, while still hidden behind a screen. Tests showed that the premature deflection was not an effect of the field of the motor on parts of the recording circuit. Nor could the premature reaction be regarded as an accidental deviation of the base line; because several subjects showed it quite regularly. For a time, it almost seemed that individuals who had often served as subjects had become conditioned to the slight noise which accompanied the transportation of the object, and that, as a consequence, weak "visual responses" began to flow when this auditory signal was heard. But the premature response also occurred when first records were taken from new subjects. Record *2* shows the paradoxical effect quite clearly. The record was taken when a black bar, 2.5 cm wide, moved across the subject's otherwise bright visual field. The marks on top indicate when the object first began to move (M), and then when it appeared in the field, when it passed the fixation mark, and when it finally disappeared. The response is of a kind frequently encountered in such records. It reaches its maximum at about the time the object passes the fixation mark, and then weakens in the second half of the field (Köhler, Held and O'Connell, '52, pp. 307 ff.). More interesting in the present connection is the fact that the response begins at point M, that is, when the not yet visible object starts on its path.

Eventually, the premature response proved to be an auditory current caused by the weak noise which the object produced as it began to move. We will presently show experimental evidence that this is the right explanation. But before we do so, the explanation must first of all be given a more specific form. When the premature response occurred, the active electrode was placed over the cortical fovea, and the grounded electrode on the vertex. How can an auditory current be registered when the electrodes are so far removed from the auditory cortex? Obviously, the issue which is here raised is no longer restricted to the very special phenomenon to which our explanation directly refers. If the premature response is actually an auditory current, then our views as to the extent to which cortical currents spread in the brain have so far been far too conservative.



Record *2* Subject F. Response of the visual cortex to a moving object. The deflection begins at M, when the object is not yet seen, but a noise caused by its movement is first heard. The active electrode is placed over the cortical fovea, and the grounded electrode on the vertex.

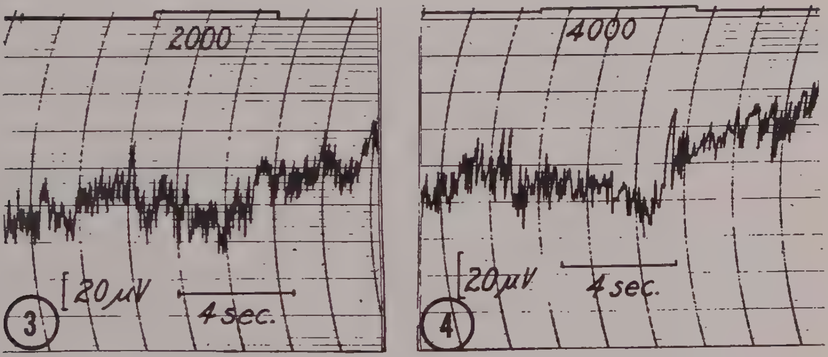
In man, the auditory area is located in the lower wall of the Sylvian fissure. The area extends from the temporal surface of the brain into the interior of the fissure, and faces mainly upward. It is our thesis that, if a part of it becomes active under the influence of sound, a current flows through this part approximately at right angles to the main orientation of the active tissue. Now, only such lines of flow as emerge on the surface of the head can influence an electrode which is attached to the scalp. Consequently, the best location for such an electrode must be the place at which these lines first appear on the surface. For, on the surface, the difference between the potential at the source and the local potential is necessarily smaller for this particular place than it is for any surface points through which the lines of flow pass later. More specifically, lines of flow which issue from an active part of the auditory cortex must distribute themselves as follows. Those which pass through the source near its boundaries must soon bend around these boundaries, and return to the other side of the source in short loops. The size of the loops must grow when lines are considered which issue from more interior parts of the action region. All lines of flow must stay within the head excepting those which pass through the middle of this region. The latter emerge on the surface of the scalp, and then envelop all others as they now spread in all directions, and eventually return to the other side of the source (Köhler, Held and O'Connell, '52, pp. 310 f.). Hence, the part of the scalp where these particular lines of flow first reach the surface of the head is the best location for the active electrode. This part must lie more or less opposite the source. Since, roughly speaking, the human auditory cortex faces upward, the crucial part must therefore lie on top of the head. It also follows that temporal parts of the surface, however near they may lie to the source, will generally not be places on which the active electrode should be located. It should be located in this region only if certain parts of the auditory cortex (which is not, of course, a plane structure) faced more or less in this direction, and if currents were to be recorded which issue from such particular regions.

We can now return to the situation in which the premature response tends to occur when visual currents are being recorded. If we assume that this response is actually a response of the auditory cortex to the weak noise which accompanies the transportation of the visual object, then the auditory current in question would mainly affect the electrode attached near the top of the head, that is, the grounded electrode on the vertex.

For, when distances are measured along the crucial lines of flow, the active electrode, which is located on the occipital pole, is farther removed from the source. Now, in the cat, potentials at the surface of the active auditory cortex have proved to be surface-negative (Köhler, Neff and Wegener, '55), and available records of human auditory currents show the same polarity. If we can rely on this evidence, the potential of a human auditory current must gradually grow as the crucial lines of flow are followed from the source to the top of the head, and then on the surface. As a result, such potentials must be lower at the vertex than they are at the occipital pole. But this is a potential difference of the same sign as the one established at the electrodes when visual currents are recorded. Thus, if the weak noise caused by transportation of the object establishes a current of sufficient intensity, the appearance of this current in records must be the same as though a visual current were flowing. Under the conditions of experimentation used when record *2* was taken, the visual response would therefore seem to start too early, because the noise is already heard before the object can be seen.

Experimental tests of this explanation were done as follows. The electrodes were placed as they had been when record *2* and similar curves were obtained, and auditory stimuli were given while no change occurred in the visual field. In a first situation of this kind, the mechanism which produced the noise was thrown into action precisely as before, but no visual object was shown. Under these conditions, deflections occurred as soon as the noise was heard. Just as had been expected, they had the direction familiar from records of visual currents; but they were quite small, presumably because the noise was so weak. Hence, while this finding corroborates our explanation of the premature response, it also shows that the form of the visual responses registered with this location of the electrodes is not seriously affected by the intrusion of such a weak auditory component. (Incidentally, many records of visual currents have been taken when presentation of the object was not accompanied by any noise.)

Far better proof that auditory currents may affect an electrode atttached to the vertex will be found in records *3* and *4*. They show responses to loud tones of the frequencies 2,000 and 4,000 ~. When these curves were registered, the vertex electrode was still grounded. On the assumption that the potential at the surface of the active auditory cortex is negative, deflections of the direction known from records of visual currents had therefore to be expected. The curves confirm this expectation. In both records, the acting potential difference amounts to about 20 μV. The responses coincide with the period of stimulation. In record *3*, an initial short deflection upward precedes the steady deflection downward. The nature of this first reaction is obvious. It is identical with the initial positive deflections so often found in the cat's auditory responses. Its direction in the record is, just as that of the steady current, reversed only because in these experiments the flow from the source affected primarily the grounded electrode. In record *4,* a similar deflection upward occurs at the end of stimulation, possibly as a response to a click in the telephone which was used in these tests.



Records *3* and *4* Subjects H. and L. Responses to the tones 2000 and 4000 ~, recorded with the electrodes in the same positions as in record *2*. Note initial wave upward in *3*, and similar wave at the end of stimulation in *4*.

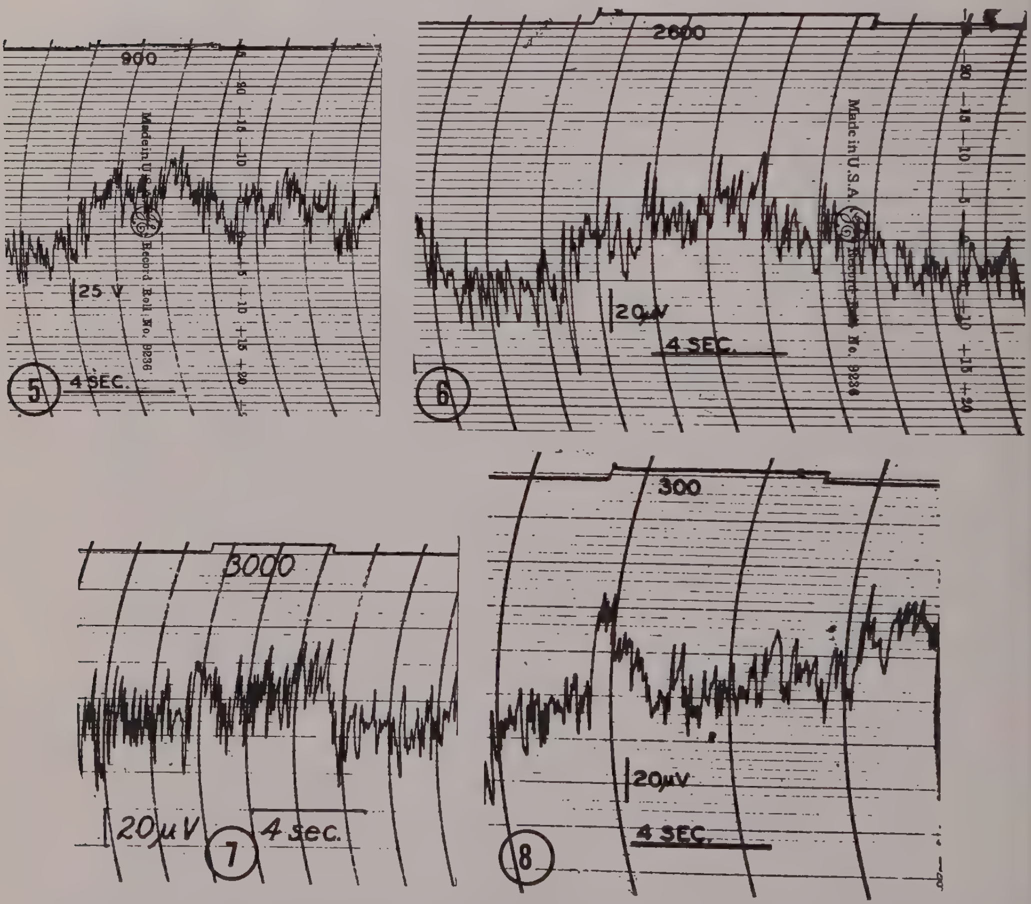
When such experiments were repeated, it was found that good records of auditory currents are much easier to obtain when the crucial electrode is attached to the top of the head than when it is given a temporal position. All further tests in this field were therefore done with the electrode in the former location. Its more precise position was, however, varied. For, while the vertex is a good location with some subjects, positions farther forward on the head gave better results with most others. In view of the fact that the Sylvian fissure slopes downward in the frontal direction, this finding is, of course, not surprising. Ordinarily, we placed the electrode on the right side of the head over areas 4 or 6 (of Brodmann's system). No accurate predictions as to its optimal location are possible because the orientation of the Sylvian fissure, and therefore of the auditory cortex, varies considerably from one individual to another. Under the circumstances, the experimenter can only try to discover the best location empirically.

The second electrode was placed either over the cortical fovea or, more frequently, on high parts of the neck. In the latter case, the heartbeat did not appear in the records so long as the position of the electrode was not too low. Since, in our previous investigations, the electrode which was primarily affected by the cortical current had always been active, we now adapted this convention also in the present work: the electrode on top of the head was made active, and the electrode attached to the occipital pole or to the neck was grounded. In the records which will presently be shown, a negative potential on top of the head, and presumably also at the source, will therefore be represented by a deflection upward.

For the most part, stimuli were produced by an oscillator, and transferred to an earphone which was suspended in the neighborhood of one ear or the other. Since we found no evidence that, with intense sounds, contralateral stimulation gives stronger responses than stimulation on the side of the active electrode, it will not be necessary in the following to indicate on which side the sounds were presented in individual experiments. Sixteen students of Swarthmore College served as subjects. From only two, no satisfactory records could be taken, although the quality and regularity of results varied also among the remaining fourteen individuals. In this report, we will show curves taken from ten subjects. All were asked to fixate a mark before them while records were taken.

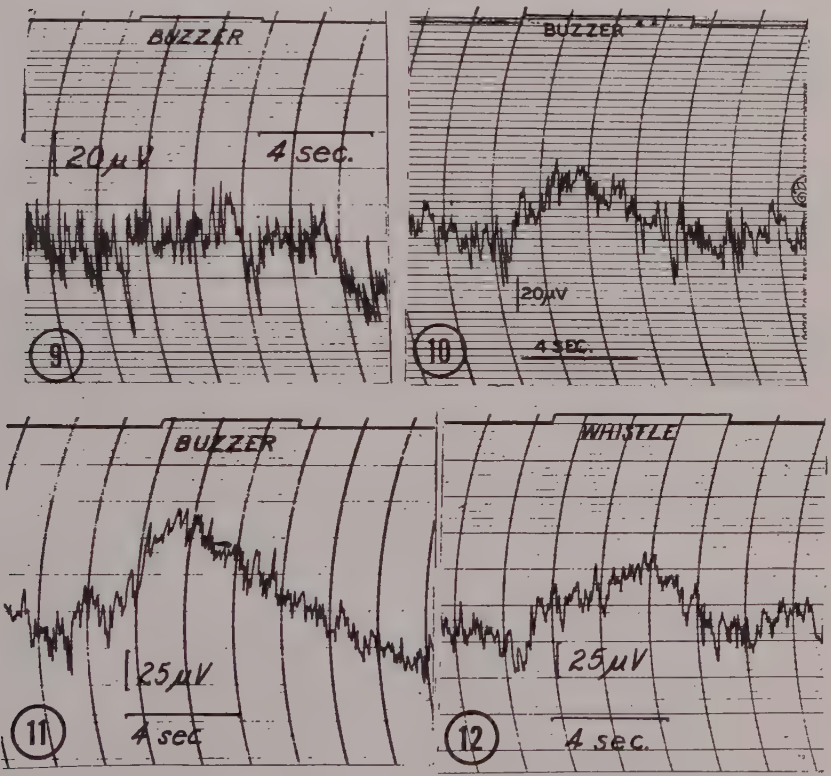
Records *5* to *7* show responses to the tones 900, 2,600 and 3,000 ∼. The curves demonstrate again that, in man just as in the cat, auditory stimulation establishes a current, the direction of which corresponds to a negative potential at the surface of the auditory cortex. In terms of voltage, the maximal size of the present responses varies from about 20 to 50 μV. In record *5*, the current reaches its greatest intensity fairly gradually, and it begins to weaken again before stimulation is discontinued. The negative deflection which follows the original response may be an after-potential. The response shown in record *6* resembles that of record *5,* excepting that in curve *6* the beginning and the end of the reaction exhibit further examples of the short positive deflection so often found when records are taken from the cat's auditory cortex. In record *7*, which is similar to record *1,* both the beginning and the end of the response are quite abrupt. Short positive waves again precede and follow the steady negative flow.

When discussing the auditory currents of the cat's brain, we pointed out that the gradual ascent of many such responses may be caused by electrotonic spread, and that electrotonic obstruction could also be involved in the gradual decline of the currents which then generally follows. We added that fatigue may contribute to the latter phenomenon. If such explanations are acceptable in the case of the cat's auditory currents, they can, of course, also be applied to records *5* and *6*. In the cat, we found, the decline of auditory responses may occur so fast that, after a few seconds, the responses disappear entirely in spite of continued strong stimulation. At the time, we remarked that, when this happens, only the potential at the active electrode may become too weak to be recorded, while in other parts the current may still be fairly strong (Köhler, Neff and Wegener, '55). The same reasoning applies to record *8* which was taken from a human head. The response shown in this curve disappears even more rapidly than the currents of records *19* and *20* in our earlier report, which were taken from the auditory area of cats. Characteristically enough, just in these records and in record *8* of the



Records *5* to *8* Subjects C., B., G. and T. Responses to the tones 900, 2600, 3000 nad 300 ~, recorded with the active electrode placed over the precentral cortex, and the grounded electrode attached to the neck. Note short positive waves in the beginning and at the end of the response in *6;* also the rapid decline of the response in *8.*

present report, the first ascent of the response is particularly steep, which may mean that in these tests the active electrode was about optimally placed. It seems plausible to assume that precisely under these conditions the potential at the active electrode will soon be strongly affected by electrotonic obstructions.



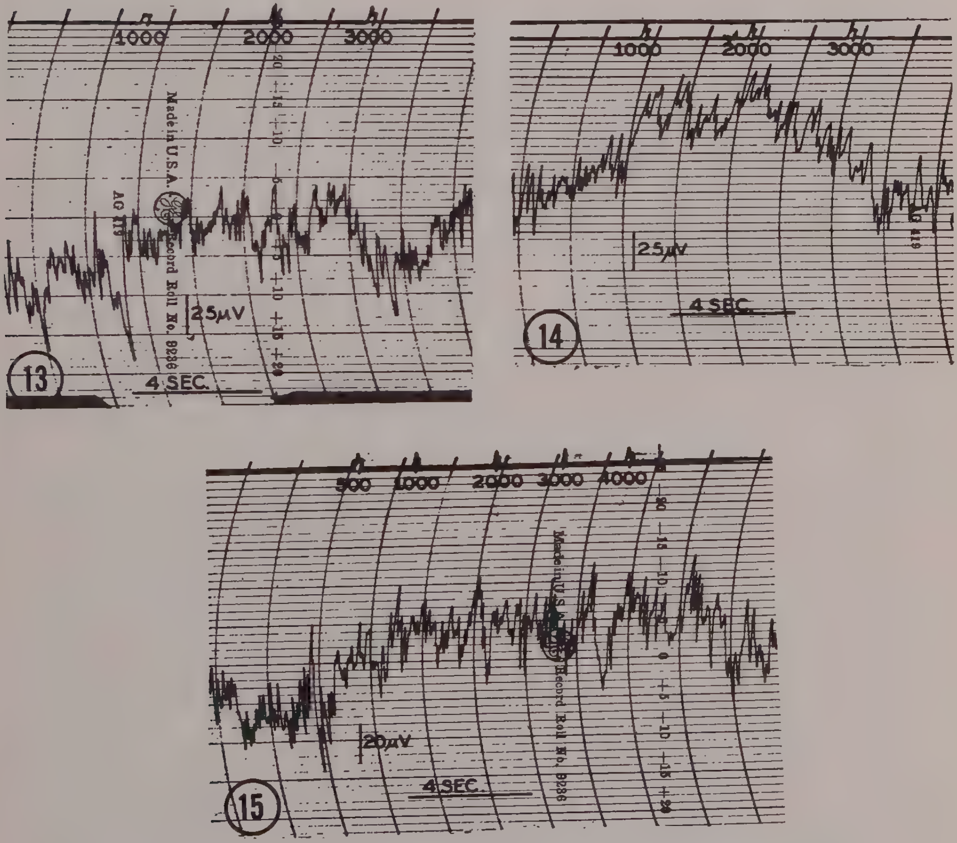
Records *9* to *12* Subjects C., Ca., T. and T. Three responses to the sound of a buzzer, and one to whistling. Position of the electrodes as in records *5* to *8*. Note the short positive waves in the beginning and at the end of the responses in *9* and *10*.

On the whole, currents of the human auditory cortex tend to be more conspicuous when stimuli are less continuous and regular than steady tones. The responses shown in records *9 to 11* were caused by the sound of a buzzer. In record *9*, the steady negative deflection is weak, but still readily recognizable, particularly since short positive deflections again appear both before its beginning and when it has ended. Records *10* and *11* show stronger responses. In record *11,* the acting potential difference reaches a maximum of approximately 60 μV. On the other hand, this response has hardly grown to maximal intensity when a fairly rapid, and more or less linear, decrease begins. Intense currents are often also established by whistling. In record *12,* the size of the response to this form of stimulation is about 50 μV at its peak.

Many records were taken when the frequency of an oscillator was changed in a continuous fashion either by hand or by a motor. Records *13* to *15* show responses to this form of stimulation. The marks on top refer to the moments at which the sweep passed the frequencies indicated underneath. In record *13,* the initial positive wave is once more conspicuous. In record *15,* a sharp descent occurs at the end of stimulation. The rise of the curve which then follows is a new deflection with the polarity of the original response. This deflection is probably an after-potential.

Records *3* to *15* seem to us conclusive with regard to a particularly important issue. One may still doubt whether the main responses shown in these curves are actually smooth potentials or, rather, smooth potentials only in appearance. But, whatever the final answer to this question may be, the present records prove that the responses of the human auditory cortex spread widely beyond their sources. For instance, since in our experiments such responses establish appreciable potentials on top of the intact head, potentials in the sensorimotor areas underneath must even be considerably stronger. To repeat, this inference does not depend upon the way in which the smooth parts of the responses will eventually have to be interpreted. For, the initial positive wave, which has for years been the best-known cortical reaction to sound stimulation, often also appears in records taken under the same experimental conditions as to the distance between the source and the active electrode. And yet, under such conditions this distance often amounts to at least 8 cm., which is a large fraction of the greatest distances to be found between two points of the human brain.

We do not believe that this finding is at variance with results previously obtained with cats. It is true that no auditory response could be recorded from the cat's visual cortex when the source was located in the auditory area, although in the cat the distance between these areas is much shorter than the distance between the human auditory cortex and the top of the human head (Köhler, Neff and Wegener, '55). But,



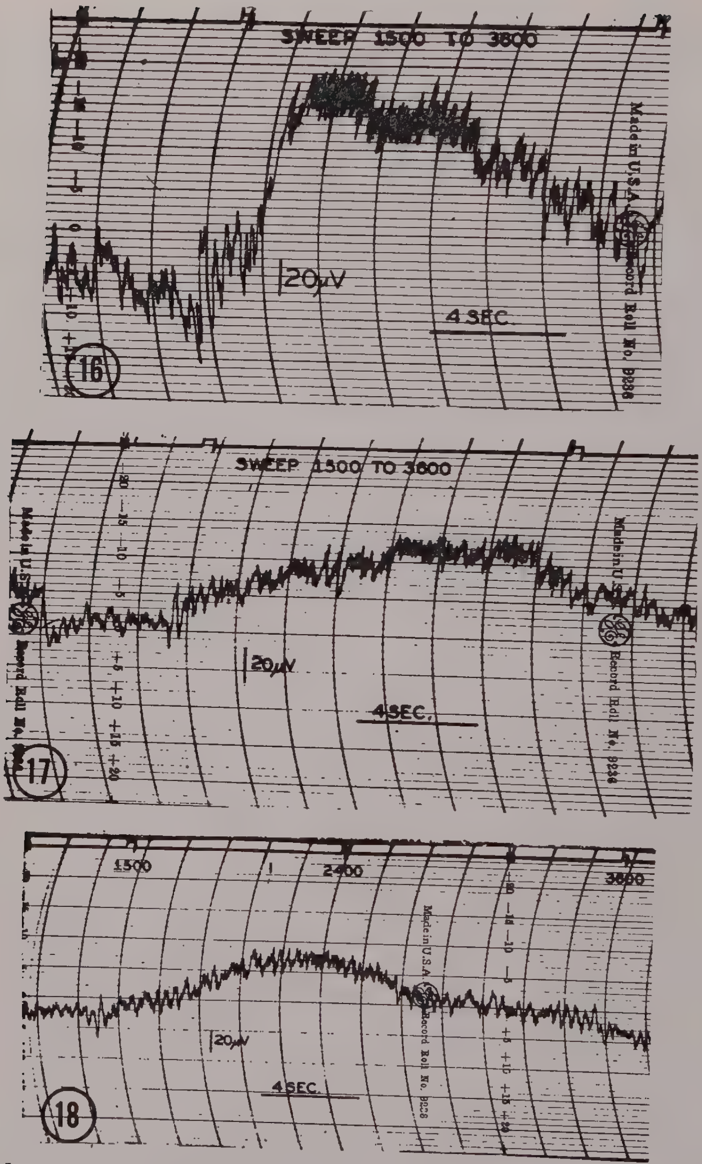
Records *13* to *15* Subjects T., T. and Ca. Responses to sweeps. Position of the electrodes as in preceding records.

as was pointed out at the time, it does not follow that the distance between these areas in the cat's brain prevents auditory currents from reaching the visual cortex. No more follows from such observations than that the potential at the part with which the active electrode made contact in such tests was approximately the same as that at the grounded electrode (which is, by definition, zero). There are always many points in the brain for which this also holds, and through which intense currents nevertheless flow. For instance, a whole isopotential surface at which the potential is zero lies between the positive and the negative side of the source. If the active electrode could be placed on this surface, no current would flow through the leads, although at the same time a strong current would pass at right angles through the same surface. Again, since the flow returns from the positive to the negative side of the source through its environment, it must on this way once more pass through places at which the potential is zero. If the part of the cat's visual cortex, on which the active electrode is located, happens to lie near such a place, practically no current will be recorded, while none the less a current of considerable intensity may flow through this part. Actually, the geometrical relation between the auditory and visual areas of the cat's small brain is such that one has difficulties in deciding whether, with the source located in the former tissue, the potential in parts of the latter should be positive or negative. It is therefore quite possible that, in those tests with cats, the potential at the active electrode differed little from zero, but that at the same time an auditory flow of some size passed through the visual cortex, which for simple physical reasons could merely not be recorded.

We will next show records of sweeps taken from the subject from whose head the visual response of record *2* (with the "premature response") had been obtained. Since this subject gave consistently good responses when the electrodes were attached to the vertex and the occipital pole, these positions of the electrodes were also chosen when the present curves were recorded; but now the vertex electrode was made active. The response in record *16* is remarkably strong; in fact, it is the strongest response which we have so far registered from a human head. At maximum, the acting voltage is approximately 100 μV. Since only the beginning and the end of the sweep are marked, we cannot say at precisely what frequency the first steep ascent occurs. During the second half of the stimulation period, the current gradually weakens.

Now, when a cat was given the same tone repeatedly, the weakening of the response during the first presentation had an after-effect in the sense that later responses to the same tone were much weaker for some time (Köhler, Neff and Wegener, '55). We made the same observation when, approximately one minute after record *16* had been taken, the present subject was again given the sweep from 1,500 to 3,600 ∼. Record *17* shows the result. The size of the greatest response is now only one-half of what it had been in record *16*. Moreover, the maximum is now displaced to a range of higher frequencies in which the current had by no means been particularly strong when record *16* was taken. When, six minutes later, the same sweep was once more presented (this time with a lower speed), we obtained record *18*. Obviously, even after this long intermission, the size of the response is still greatly reduced. In addition, its maximum has again shifted, this time back to relatively low frequencies.

The persistent after-effects of auditory stimulation are, unfortunately, highly important in a practical sense. As has been explained elsewhere, similar effects of repeated tests occur also when visual currents are being recorded (Köhler, Held and O'Connell, '52, pp. 302 f.). As a consequence, consistently good results in either field can be obtained only if considerable rest periods are given between individual trials. For obvious reasons, this rule applies especially to tests in which the same stimulation is repeatedly used. It has been our general experience that, just when a particularly strong response has been recorded, a next test which follows



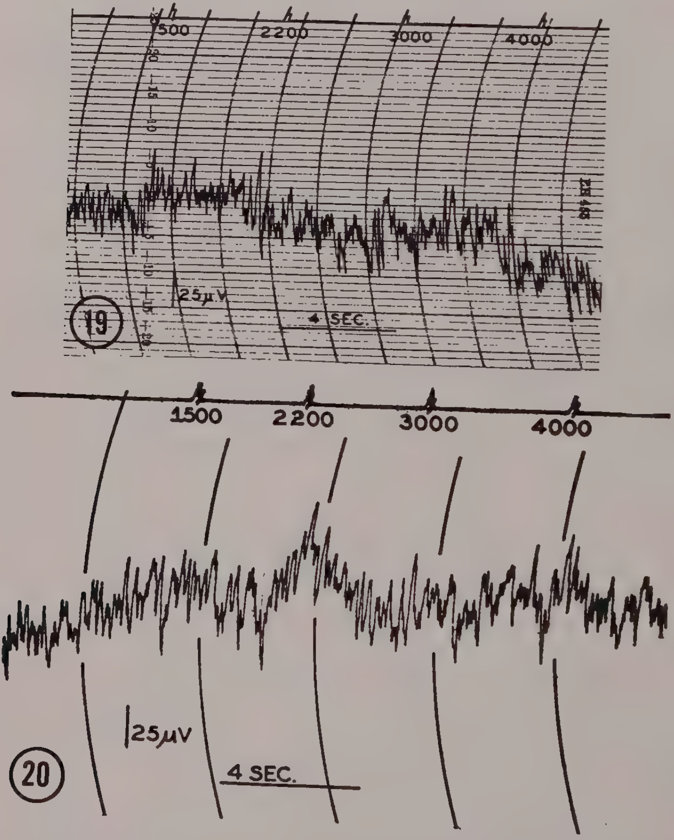
Records *16* to *18* Subject F. Responses to repeated stimulations by the same sweep, recorded with the active electrode placed on the vertex, and the grounded electrode over the cortical fovea. Repetition of stimulation reduces the absolute size of the response, and changes its relative size in parts of the sweep. Note the accentuation of the cortical rhythm in *16* and *17*.

too soon tends to give a poor result, and that, for the most part, best records are obtained after long intermissions. When record *18* is compared with records *16* and *17,* it will be seen that even a rest period of several minutes may still be too short.

The depression which follows strong stimulation makes it difficult to answer certain questions, including questions which refer to the nature of the depression itself. In the field of hearing, one would, for instance, like to know to what degree this depression is localized in terms of frequency, and it seems natural to assume that the answer to this question can be found in experiments of the following kind. When a certain tone has repeatedly been presented, a test is made in which a sweep is given. Does the response to this sweep show a localized depression in the region which corresponds to the frequency of that particular tone? Moreover, if there is such a depression, how large is the region in which it appears? On the other hand, one can first give repeated presentations of a sweep from which a certain range is omitted, connections with the earphone being interrupted while the oscillator frequencies pass through this range. If afterwards the complete sweep is given in the test, will the response be stronger in the region which has previously not been stimulated?

We have done experiments of both kinds, but results have often been disappointing, at least so far as the first of the two suggested procedures is concerned. In view of the curves shown in records *16* to *18,* the reason is obvious. The sweeps which are given in tests cause the same depression within a wide range of frequencies as the tests are meant to demonstrate in a restricted range. Moreover, when a sweep is given repeatedly, the greatest size of the response tends to shift from one part of the sweep to another, quite apart from a localized depression established by a previously presented steady tone. As a consequence, no reliable results can be expected from this procedure. We therefore refrain from showing even such curves as seem to agree with theoretical expectations.

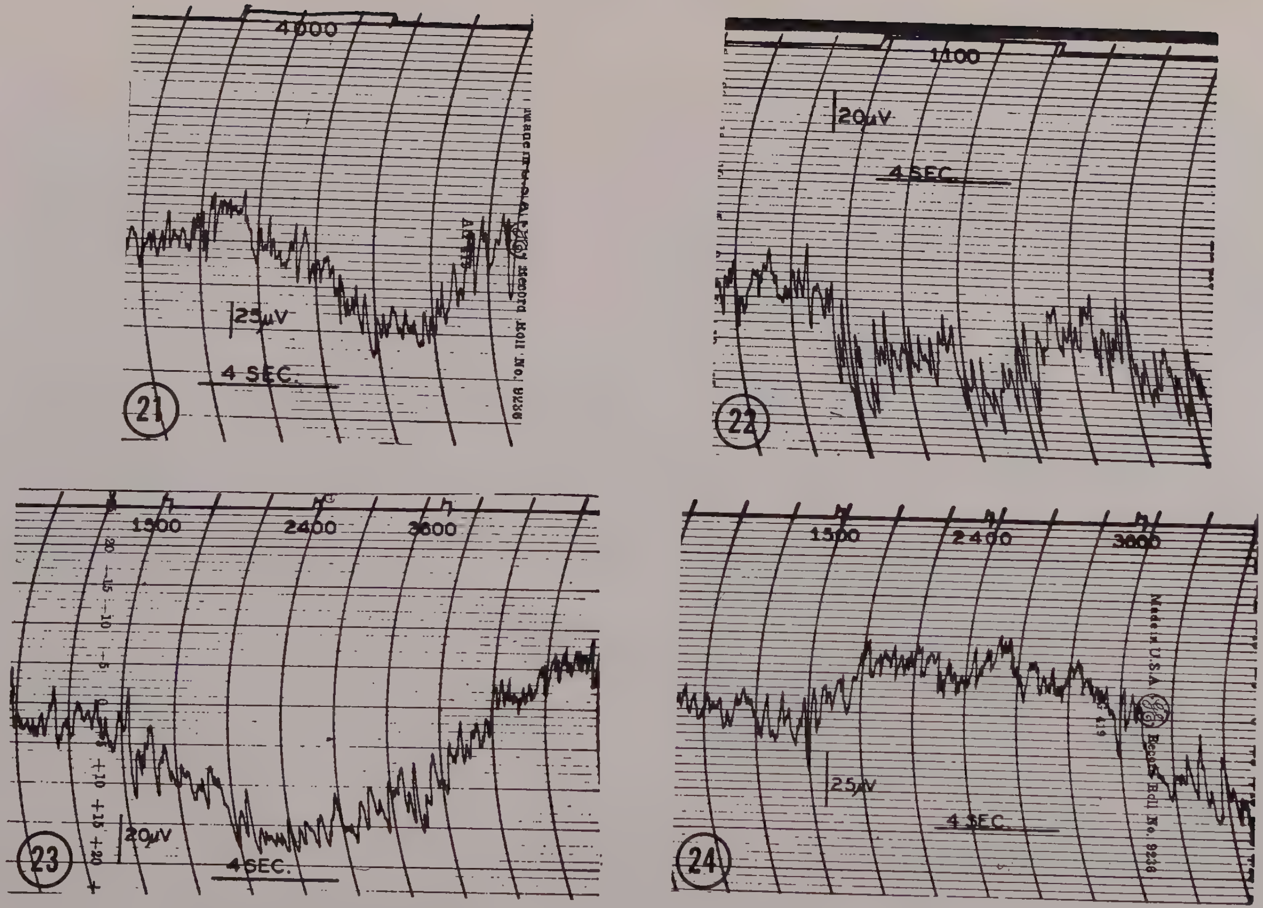
The other procedure, in which an interrupted sweep is repeatedly presented, and then followed by a complete sweep, gives sometimes entirely convincing results. Record *19* shows one of the responses obtained when an interrupted sweep from 1,500 to 2,200 and from 3,000 to 4,000 ~ was presented.



Records *19* and *20* Subject Fi. The sixth response to an interrupted sweep (silent period from 2200 to 3000 ~), and the response to the complete sweep (1500 to 4000 ~) after four further presentations of the interrupted sweep. Note the interruption of the response during the silent period (in *19*), and the corresponding maximum in the response to the complete sweep (in *20*). The active electrode is placed over precentral cortex, the grounded electrode attached to the neck.

Before this record was taken, the same sweep had already been given five times. In record *19,* responses to the first and the second part of the sweep are therefore weakened by these preceding presentations. Nevertheless, both are still recognizable, and a dip between them, which corresponds to the silent period from 2,200 to 3,000 ~, is also fairly obvious. After four further presentations of the interrupted sweep, during which hardly any convincing responses to its two parts were registered, a complete sweep was given in a test. The result is shown in record *20.* The only clear response which appears in this record lies between the frequencies 2,200 and 3,000 ~, that is, in the formerly silent period. The form of this response suggests that the depression caused by the interrupted sweeps extends on both sides into the crucial range. For, the deflection upward is really conspicuous only within a small part of this range. Incidentally, record *20* once more proves that the depression caused by repeated stimulation persists for considerable periods. The record was taken three minutes after the last interrupted sweep had been given. Nevertheless, after this interval there are still no responses in the two affected regions.

If, in spite of an already existing strong depression, stimulation is further repeated, records finally show an effect which is never observed when (with the electrodes placed as indicated) subjects have not yet served in many experiments. The polarity of the responses now tends to be reversed. The effect is clearly caused by overstimulation because, after a rest period of sufficient length, currents registered in further tests flow again in the normal direction. Record *21* shows a response to the tone 4,000 ~ which was given at maximal volume after a great many tests with sweeps had previously been done. The size of the responses to these sweeps had gradually decreased. In record *21,* a first short deflection in the usual negative direction is followed by a strong deflection in the positive direction. The general form of this curve is the same as that often obtained when the active electrode is given a temporal location, and the grounded electrode is at-



Records *21* to *24* Subjects T., B., F. and F. Responses to the tones 4000 and 1100 ~ (*21* and *22*) and to sweeps (*23* and *24*) after many stimulations. Note the reversed polarity in records *21* to *23*, and the return to normal polarity after a rest period in *24*. Electrodes placed over precentral cortex and in the neck with subjects T. and B., on the vertex and over the cortical fovea with subject F.

tached to the vertex (Köhler, Held and O'Connell, '52, p. 324). But in the present experiment the active electrode was placed in front of the central fissure, and the grounded electrode on the neck.

Sometimes, as in record *22,* the current shows the reversed polarity at once. This curve was also registered after a great many others tests with intense sounds. The polarity of the registered flow may be reversed for the whole duration of a sweep. Record *23* is a good example. It was taken from the subject whose earlier responses to sweeps have been shown in records *16* to *18.* The active electrode was still attached to the vertex, and the grounded electrode was placed over the cortical fovea. After those earlier experiments, the subject had been given whole series of tests with sweeps from 1,500 to 3,600 ∼. The response shown in record *23* has throughout the positive polarity. This extreme effect of overstimulation did not, however, persist for long. When seven minutes later the same sweep was given, the result was record *24,* in which the response has the normal polarity.

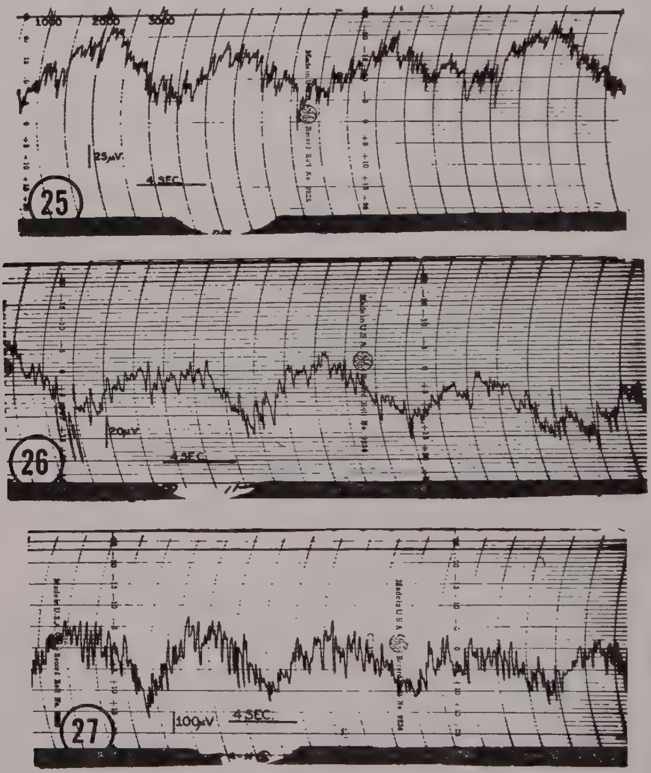
An explanation of such reversed potentials can again be given in terms of electrotonic obstructions which are built up when strong auditory currents pass many times through the tissue between the auditory cortex and the active electrode. If such obstructions grow to greater size than those which are established in other parts of the circuit, the distribution of potential differences must gradually change as follows. The difference between the negative potential at the surface of the auditory cortex and the potential at the active electrode must be increased, and thus the potential at this electrode must gradually approach the zero potential of the grounded electrode. As a consequence, the registered current must be weakened, and since the obstructions which currents establish in the brain survive the disappearance of these currents, the persistent depressions discussed in preceding paragraphs will be observed. When the potential at the active electrode has actually been raised to zero, no current will, of course, be recorded. There is no reason why, when the obstruction grows still further, the potential at the electrode should not be raised above zero. If this happens, a current will again be registered, but the polarity of the recorded flow will now be reversed. The reversal may, of course, occur while a record is being taken. In this case, curves such as that of record *21* will be registered. This record shows, however, that the present explanation is not yet complete. For, in this curve, the positive deflection persists for several seconds beyond the end of stimulation. It seems to us a possible assumption that, when strong obstructions have arisen, currents of depolarization will tend to issue from the obstructed parts. Their direction would be opposed to that of the primary auditory currents, and they could continue to flow when the source in the auditory cortex is no longer active. Strong currents of depolarization may also explain the fact that, when the obstructions have become sufficiently great, the now reversed potential is relatively soon replaced by a potential of the normal sign (*cf.* record *24*). Incidentally, if our explanation of the reversals as such is correct, it need not be assumed that, when the potential difference between the two electrodes is reversed, the direction of the voltage at the source in the auditory cortex is similarly changed.

* * *

We have to add one more remark about the curves which have so far been shown. None of these curves contains evidence that sound stimulation blocks the rhythm of the auditory cortex. In this respect, the present records agree again with the records taken from the cat's auditory cortex (Köhler, Neff and Wegener, '55). Under the circumstances, one may expect that, just as in the cat, sound stimulation has the opposite effect, in other words, that sounds accentuate the rhythm of the human auditory area. We have already explained why, if this is actually the case, the fact would generally not appear in records taken with our instruments. But it does appear occasionally, precisely as it did when the auditory currents of cats were being registered. The phenomenon is obvious in record *16*, and present also in record *17*. We are, of course, assuming that the change of the rhythm which is shown in these curves occurs in the auditory cortex rather than in the cortical tissue over which the active electrode is placed.

We now turn to a last observation made in our study of human auditory currents. When subjects have been given many tests, very slow waves are sometimes recorded in the absence of any corresponding stimulation. The same phenomenon also ocurred when currents of the human *visual* cortex were investigated (Köhler, Held and O'Connell, '52, pp. 322 f.). It was then found that the waves originated more readily in some subjects than in others. Once they had appeared, they could often be recorded for long periods. In the present investigation, these findings were confirmed. Only with four of our subjects did the phenomenon become conspicuous; but with these it tended to be highly persistent. Records *25* and *26,* which were taken from different subjects are good examples. In record *25*, the waves follow the response to a sweep, and obviously resemble this response. Record *26* was taken when only one presentation of a steady tone had followed a rest period of ten minutes. But before this intermission many other sound stimulations had been given, and waves of the same kind had repeatedly developed during these tests. Incidentally, such waves appeared also in records taken from one of the cats whose auditory responses we have investigated (Köhler, Neff and Wegener, '55). Record *27* does not immediately show that it was taken from a cat's rather than from a human head. Actually, the only difference is that in this record the over-all amplitude of the waves amounts to several hundred μV. When the waves were registered, the active electrode was placed on the intact skull over the auditory area, and the grounded electrode on the neck.

The length of the waves often agrees with the average length of preceding stimulation periods; but, since this is not always the case, the agreement may be accidental when it occurs. Actually, even the origin of the phenomenon is still unknown. The waves may be after-effects of frequent strong stimulations, and may arise in parts of the brain which have been affected by such stimulations. So far, we have no proof that this is true. In fact, an entirely different interpretation might be suggested. During experimental sessions, subjects cannot move very much; and, as a result, strains will often develop in their sensorimotor apparatus. A cat who is kept in a holder, with his limbs fastened to a board, is obviously in a similar situation. If it were argued that the waves shown here and in an earlier report might represent reactions of the sensorimotor system to such conditions, we could offer no conclusive evidence against this suggestion. It is for this reason that we make no attempt to relate the slow waves to the obstructions



Records *25* to *27* Subjects T., Fo. and cat 11. Slow waves recorded in the absence of stimulation after prolonged experimentation.

which are caused by repeated visual or auditory stimulation as such.

DISCUSSION

The following remarks refer not only to the results which have just been described but also to the issue of smooth cortical potentials in general.

Such potentials can be recorded only when three conditions are fulfilled. A *first* condition is obvious. The amplifying devices used for this purpose must be such that, in their output, potentials of considerable duration are not automatically eliminated. With most capacity-coupled amplifiers such potentials cannot be registered unless a breaker is introduced in the circuit. Apparently, this has seldom been done, on the assumption that all important responses of the central nervous system have the form of short-lived waves.

Secondly, stimulation periods must be sufficiently long. The light flashes and clicks which are often used in studies of evoked potentials are obviously too short to permit the development of smooth responses.

The *third* condition which must be fulfilled refers only to work with animals. Evoked potentials are fairly resistant to anesthesia. On the other hand, the currents of the projection areas are highly sensitive to anesthetic action. The fact that anesthesia must be light if smooth cortical potentials are to be registered is, of course, inconvenient from a technical point of view. For, under these circumstances, movements of the experimental animal will sometimes disturb the recording.

We enumerate these conditions for the purpose of explaining why smooth responses of cortical projection areas to peripheral stimulation have not been found in previous investigations, a fact which would otherwise seem to argue against our own results. It is true that one or sometimes two of the conditions necessary for the recording of smooth responses have been fulfilled in some earlier investigations. Thus, some experimenters have used direct-coupled amplifiers, some have given stimuli of considerable duration, and Bremer's procedure of the *encéphale isolé* avoids the use of general anesthesia entirely. But the direct currents of the projection areas can be registered only when the three conditions to which we have referred are simultaneously present in a given experiment. To our knowledge, this has rarely been the case in earlier studies. The fact that no steady cortical responses have been found in these studies does, therefore, not argue against their existence.

The finding that cortical currents are highly sensitive to anesthesia differentiates between these currents and certain other neural processes. We have been asked whether the steady deflections shown in our records might not be envelopes of afferent nerve impulses which our slow recorder cannot register as individual events (Köhler, '51). This interpretation is probably no longer possible. The arrival of nerve impulses in the cortex is announced by evoked potentials. Now, these potentials can still be registered, and therefore the impulses still arrive in the cortex, when anesthesia is so deep that no smooth deflections can be recorded. Obviously, if the interpretation were correct, the smooth deflections should not disappear until the evoked potentials are also strongly affected. It may be much more difficult to decide whether the steady deflections can be explained as envelopes of cortical rather than of afferent impulses.

In the meantime, the question may be raised whether, if the smooth deflections should prove to be genuine records of smooth currents, their origin could be related to more familiar physiological knowledge. The following remarks, which must be regarded as tentative, refer to one such possibility. In 1936, Barron and Matthews ('36) demonstrated that, under the influence of afferent impulses, the gray tissue of the spinal cord develops potentials of considerable size and duration. Since this discovery, the same authors and others have shown that the potentials in question are established at synapses, and at the present time it seems to be the generally accepted view that, more particularly, they represent reactions of post-synaptic cell membranes to the arrival of impulses in pre-synaptic nerve endings. Since the size of synaptic potentials in this sense grows by summation when the frequency of incoming volleys is increased, the potentials do not follow the all-or-none principle. Beyond a certain frequency of the volleys, the potentials appear to become quite smooth.

Potentials of this kind have since been discovered in various species and at synapses in several parts of the nervous system, including the endplate of muscle, the potentials of which are now generally included in the same category. So far it has not yet been demonstrated that synaptic potentials are also established at cortical synapses. But in present discussions it is sometimes taken for granted that they are.

If we use the language of physics, potentials which are registered in the neighborhood of synapses must derive from electromotive forces located at the synapses themselves. In other words, the potentials are those of currents which flow through the post-synaptic cell membranes, and then return to the other side of these sources through the environment. This view is supported by the fact that the potentials registered at some distance are increased by electrotonic spread.

In connection with our own work, the following conclusion is of particular interest. The currents which issue from synapses must be about as smooth and persistent as the electromotive forces by which they are maintained. When, under the influence of peripheral stimulation, synaptic potentials arise at large numbers of adjacent synapses, the distribution of the resulting currents must be the same as that of the currents assumed by us to flow in cortical projection areas when parts of corresponding sensory surfaces are stimulated. The currents must be most intense near the boundaries of the active region where the lines of flow are shortest, and they must be progressively weaker as lines are considered which issue from more and more interior parts of the region. Along lines of flow which issue from the center of this area, and then envelop all others, the intensity of the flow must be smallest. There is no difference between this pattern and the one which Gerard and Libet have attributed to their cortical fields (Gerard, '41; Gerard and Libet, '40; Libet and

Gerard, '41). The pattern also agrees with that of the currents postulated by Köhler and Wallach ('44), and then, presumably, demonstrated in our later studies.

Under these circumstances, one feels tempted to assume that the smooth deflections shown in these studies represent currents which are mantained by synaptic electromotive forces of cortical projection areas. Whether this assumption is acceptable can be decided only by the results of further investigations. For it remains to be shown that such currents have the persistence and the size indicated by our results. Since synaptic potentials are mostly magnified by amplifiers with a time constant of only a few seconds, and since the periods of stimulation used in such experiments have also been rather short, no final answer as to the persistence of synaptic potentials can be given at the present time. We merely know that, under the influence of frequent afferent volleys, the size of the potentials may remain fairly high for periods of more than a second. Actually, this size is often very great. Even when the electrodes are not given optimal positions, potentials of several mV are sometimes recorded. It therefore seems safe to assume that the extent to which synaptic currents spread in the environment of their sources is often considerable. It may nevertheless be doubted whether the results of the present study can be interpreted in such terms. For it will be remembered that we have taken records of human auditory currents when the distance of the active electrode from the source amounted to about 8 cm.

More generally speaking, it is, of course, dangerous to assume that findings concerning the synaptic potentials of the spinal cord, and so forth, simply apply to the assumed synaptic potentials of the cortex. Further discussion of the present issue must therefore be postponed until actually pertinent evidence is available.

SUMMARY

1. Records of human auditory currents greatly resemble those taken from the cat's auditory cortex. Both indicate

that the potential at the surface of the active cortical tissue is negative.

2. In spite of the great distance involved, the records shown in the present report have been taken when the active electrode was placed on top of the head. It seems that the auditory flow first reaches the surface of the head in this region.

3. Repetition of stimulation soon reduces the size of the registered responses. The depression may persist for long periods. When, under these circumstances, stimulation is further continued, the polarity of the registered currents may temporarily be reversed. This fact can be explained in terms of electrotonic obstructions and corresponding redistributions of potentials.

4. No evidence has been found that sound stimulation blocks the rhythm of the human auditory cortex. Occasionally, auditory stimuli accentuate the rhythm.

5. After prolonged experimentation, very slow waves are sometimes recorded in the absence of stimulation. They resemble the waves previously found after prolonged recording of human visual currents. The origin of the waves has not yet been discovered.

6. The question whether cortical currents are maintained by potentials which afferent impulses establish at cortical synapses cannot yet be answered. So far there is no evidence that the spread of currents which issue from synapses is comparable to the spread of human auditory currents.

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